THE MACROURIDAE OF THE WESTERN NORTH ATLANTIC AND CENTRAL AMERICAN SEAS

By Albert E. Parr

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ABSTRACT

Keys for identification, descriptions and illustrations are given for all species of Macrouridae occurring in the western North Atlantic and in the Central American Seas. The subfamily *Steindachnerinae*, the genera *Grenurus*, *Cariburus*, the subgenus *Pawnurus*, and the species *Ventrifossa atlantica*, *Nezumia hildebrandi*, *Grenurus grenadae* and *Cariburus mexicanus* are described as new. While distinctions between other genera may be made on the basis of whether the anus and genital pore have been advanced below the abdomen or remain at the origin of the anal fin, a third type of situation is shown to exist in *Steindachneria*, in which case the anus is advanced while the genital pore remains at the anal fin so that the two openings are widely separated.

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INTRODUCTION

In the present paper the author will not attempt to deal with the species occurring outside of North and Central American waters. Nevertheless, in attempting a classification of these western Atlantic species it has been found necessary to effect some modifications and innovations in the system by which they are arranged. With such geographic limitation this procedure might seem hazardous, and therefore the conclusions are not presented with any claims to finality. But it seems evident that the macrouroid species, and even many of their genera, are definitely not cosmopolitan in the manner of so many of the pelagic fishes, a fact which was clearly recognized for the first time by Gilbert and Hubbs (1920) in their discussion of macrouroid fauna-regions within the Pacific alone. Under these circumstances it seems perfectly permissible to attempt to work out a logical and practical system of classification for a single region; this can subsequently be integrated with similar systems for other faunas. At least it appears to the writer almost impossible to advance beyond the great groundwork laid down by Gilbert and Hubbs (1916, 1920) until much more detailed studies of apparent relationships within smaller faunal units have been made and published.

The following discussion and descriptions are, therefore, intended to serve a dual purpose, namely, 1) to develop a practical method of arriving at the specific identities of the western Atlantic forms within the framework of a reasonable generic classification which is reliable in its practical application to the fauna of the region concerned, and 2) to attempt to contribute to the refinement of general classification by designing the system of local classification so that it will be capable of integration with other restricted systems towards ultimate generalizations.

In regard to the arrangement of the genera in subfamilies, the author has only one suggestion to add to those already made by Gilbert and Hubbs. An examination of the topographical anatomy of the abdominal cavity has revealed a peculiar condition in *Steindachneria*, which, when considered with the previously known peculiarities of this genus, apparently demands the introduction of a separate subfamily. Among the other macrourids the anal opening may be found either at the origin of the anal fin or advanced to an anterior position widely separated from the anal fin base. But in all these other forms the genital pore is closely associated with the anal opening, whatever its position may be. In *Steindachneria* the anal opening is so advanced as to lie immediately behind the ventral fins, while the genital pore remains at the origin of the anal fin. This is the only known case among the macrourids in which such a separation between anal opening and genital pore is found.

The subfamilies Lyconinae, Macrouroidinae and Ateleobrachinae are without representatives in the western North Atlantic and therefore are not included in this report. The subfamilies Bathygadinae and Coryphaenoidinae will be further analyzed at the proper points in the following discussion.

REMARKS ON KEYS

It seems impossible to devise a key combining the greatest ease and convenience of use with the proper arrangement of the genera in terms of their probable relationships. In the keys presented herewith, systematic arrangement has been sacrificed for the attainment of mechanical simplicity in the manipulations and observations required to place any specimen in its proper genus. The most conspicuous instance of such a sacrifice is in the use of serrate or smooth dorsal fin, rather than the number of branchiostegal rays, at an early point in the key. In small specimens, or in specimens in which the upper branchiostegal is held firmly in a hidden position, or in which the lower branchiostegals are of reduced size, a reliable count of these rays may require dissection; this can be done easily without great damage under the favorable conditions of the laboratory, but it may be decidedly inconvenient in the field or in the preliminary sorting of large collections. The main disarrangements of positions in terms of probable relationships resulting from this procedure are those to be found in the wide separation of *Malacocephalus* from *Leucomacrurus*, and perhaps likewise in the separation of *Trachonurus* from *Cetonurus*. On the other hand, it is not evident that a major division by number of branchiostegal rays would remove all discrepancies between natural relationships and arrangement in the key.

Family MACROURIDAE

Key to the subfamilies represented in the western North Atlantic[1]

1a. 2nd dorsal fin better developed than anal fin. First gill slit not restricted. Gill rakers not tubercular. Second ray of 1st dorsal fin not modified or spine-like. Vomer with or without teeth.

  2a. Teeth on vomer. Anterior portion of anal fin forming a produced lobe. Teeth in jaws in 1 or 2 series. Anus immediately behind bases of ventral fins. Genital pore at origin of anal fin, widely separated from the vent. STEINDACHNERINAE

  2b. Vomer without teeth. Anterior portion of anal fin not produced. Teeth in jaws in bands. Genital pore immediately behind anus, at origin of anal fin. BATHYGADINAE

1b. Anal fin better developed than 2nd dorsal fin. First gill slit restricted by a fusion of the dermal cover of the lower part of the first gill arch with the inner lining of the floor of the mouth. Gill rakers very short and tubercular. Second ray of 1st dorsal fin modified into a spine. No teeth on vomer. CORYPHAENOIDINAE

STEINDACHNERINAE, new subfamily

Characters as shown in preceding key. Distinct from all other macrourids by the wide separation between anus and genital pore. Only one genus.

Genus **STEINDACHNERIA** Goode and Bean, 1895

Steindachneria Goode and Bean, in Agassiz, 1888, *15:* 26; Goode and Bean, 1895: 419; Gilbert and Hubbs, 1916: 139 (in key).
Steindachnerella Eigenmann, 1897: 159.
Not *Steindachneria* Eigenmann and Eigenmann, 1889: 137.

2nd dorsal fin high and well developed, its rays fully united by membrane. First 10–12 rays of anal fin fully developed and united by membrane to form an anterior lobe of about the same height as anterior portion of 2nd dorsal fin. Remaining rays of anal fin small and separate, without continuous membrane. 1st dorsal fin with smooth, produced first ray, but otherwise less developed than anterior portion of 2nd dorsal. Ventrals moderate, with produced ray. Pectorals large. Anus and genital pore widely separated, the anus immediately behind ventral fins, the genital pore only a short distance in advance of origin of anal fin. About 18–20 simple pyloric caeca. Intestine relatively short, in a single, simple backward loop. Gill slits wide, not restricted by membrane attached to first arch. 7 branchiostegal rays. Interoperculum thin, but large and broadly exposed below preoperculum. Gill rakers long, slender, about 12–15 on lower limb of first arch. Teeth in anterior half of upper jaw in a single series, of relatively large, very wide-set fangs; this series continued posteriorly as a series of small, close-set teeth well inside of a second outer series of larger wide-set teeth, which extends forward only to about middle of jaw. Two types of teeth also in lower jaw; a relatively small number of large, very wide-set fangs, and a large number of minute teeth, but since the two types are not arranged in well separated lines they can be said to form neither two distinct series nor a single series together. Teeth also present on vomer. Ventral area of trunk and tail with a characteristic pattern of transverse or vertical striations which become conspicuous only under magnification. Head moderate, of gadoid appearance. Mouth large, lateral and subterminal. No barbel. Eyes large, lateral. Scales moderate to large, very deciduous, thin and cycloid (*fide* Goode and Bean). No scales seen by the writer.

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[1] This key is essentially a modified abstract of that given by Gilbert and Hubbs (1916: 139).

Only one single species of apparently very restricted distribution.

Steindachneria argentea Goode and Bean, 1895

Figure 1.

Steindachneria argentea Goode and Bean, 1895: 419, fig. 351; Jordan and Evermann, 1898: 2568; 1900: fig. 909; Jordan, Evermann and Clark, 1930: 203.

General Characters. Head moderate, gadoid in general appearance, about 20% of total length in complete specimens. Trunk fairly long; distance from snout to anal fin about 30–32% of total length, 50–70% longer than head. Head and body moderately compressed, the dorsal and ventral outlines tapering gradually into tail. Greatest depth about 80% of length of head. Abdominal cavity extending beyond origin of anal fin for a distance equal to about 20–25% of head. 18–20 simple pyloric caeca.

Scales. Rather large, very deciduous (none seen by writer), about 25–30 in a longitudinal row from shoulder over a distance equal to that from snout to 1st dorsal fin.

Head Characters. Dorsal profile of head behind snout almost straight. Snout not prominent, low, rounded; length from orbits about 20% of head. Mouth large, lateral, terminal, slightly oblique. Upper jaws 50–55% of head, extending to below middle of eyes. Eyes large, lateral, circular; diameter of orbit about 27–28% of head. Interorbital width 18–20% of head, 1.5 in orbit. Preopercle's posterior free margin slightly inclined forward and upward, its lower corner broadly rounded. Longest gill rakers about 15–17% of head; about 12–15 on lower limb of first arch.

Teeth. As described for the genus.

Fins. Origin of 1st dorsal vertically above origin of pectorals, with origin of ventrals also on approximately the same vertical, but with somewhat wider range of individual variation. 1st dorsal fin moderate, with produced first ray reaching about 60% of length of head; length of second ray about 30–35%; distance from snout to 1st dorsal fin about equal to length of head. Origin of

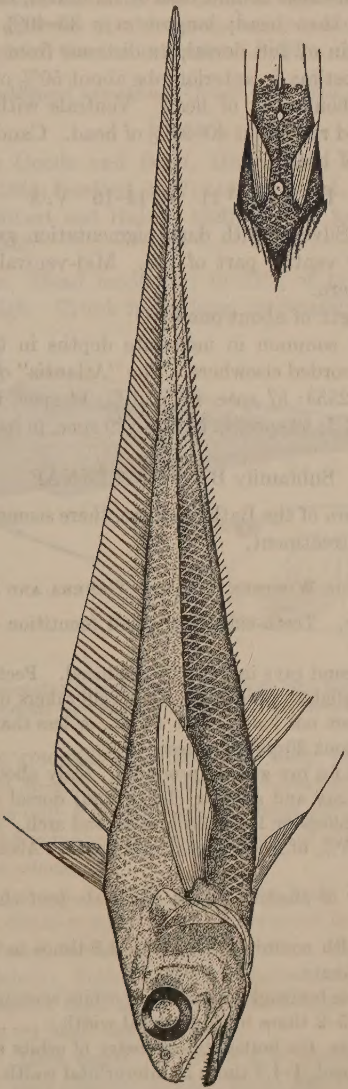

Figure 1.—*Steindachneria argentea* Goode and Bean, with ventral view showing anal and ventral fin area.

2nd dorsal fin a short distance behind base of 1st dorsal, its distance from snout about 30–35% longer than head; longest rays 35–40% of head. Anal fin origin well behind origin of 2nd dorsal, its distance from snout about 65–75% longer than head; longest ray in anterior lobe about 50% of head; distance from ventrals to anal fin about 70% of head. Ventrals with produced first ray, 75–85% of head; second ray about 40–50% of head. Caudal fin's ultimate rays rather long, 10–15% of head.

D_1. 9 A_1.[2] 11 P. 14–15 V. 8

General coloration. Silvery, with dark pigmentation gaining ascendency on abdomen and anterior ventral part of tail. Mid-ventral portions with characteristic striated pattern.

Size. Reaches a length of about one foot.

Range. Apparently common in moderate depths in the northern Gulf of Mexico, but not yet recorded elsewhere. The "Atlantis" obtained the following samples from Station 2853: 57 spec. in haul C; 14 spec. in haul D; 8 spec. in haul F; 31 spec. in haul J; 56 spec. in haul K; 29 spec. in haul L.

Subfamily BATHYGADINAE

In regard to the genera of the Bathygadinae, there seems to be nothing to add to Gilbert and Hubbs' treatment.

Key to the Western Atlantic Genera and Species

1a. Barbel long, slender. Teeth extremely small (dentition chagrin-like). Genus *Gadomus*
  2a. Both first and second rays in ventrals produced. Pectorals with 21–25 rays, the upper ray slightly produced. 18–20 gill rakers on lower limb of second arch. Gill rakers not long (about 4 mm., or less than 5%, of head in large specimen). About 30 pyloric caeca. ***G. arcuatus*, p. 9**
  2b. Only first ventral fin ray greatly produced. Only about 14–16 pectoral rays; upper pectoral ray and anterior (1st or 2nd) dorsal rays greatly produced. About 28 gill rakers on lower limb of second arch. Gill rakers long (about 6 mm., or 12–15%, of head in small specimen). About 10–12 pyloric caeca. ***G. longifilis*, p. 10**
1b. Barbel rudimentary or absent. Teeth moderate (not chagrin-like). Genus *Bathygadus*
  3a. Interorbital width contained less than 3.5 times in length of head. Eyes small or moderate.
    4a. Eyes small, the horizontal diameter of orbits contained 5–6 times in length of head; 1.5–2 times in interorbital width. . . . . ***B. favosus*, p. 12**
    4b. Eyes moderate, the horizontal diameter of orbits contained 3–4 times in length of head; 1–1.3 times in interorbital width. . . . . ***B. vaillanti*, p. 14**

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[2] Anterior lobe, counting only rays comprised within its outline and connected by its membrane.

3b. Interorbital width contained 4–5 times in length of head. Eyes large, the horizontal diameter of orbits contained only about 3 times in length of head, or 0.6–0.7 times in interorbital width.........*B. macrops*, p. 16

Gadomus arcuatus (Goode and Bean, 1886)

Figure 2.

Bathygadus arcuatus Goode and Bean, 1886b: 158; 1895: 421; Jordan and Evermann, 1898: 2564; Koefoed, 1927: 114, fig. 39, pl. VI, fig. 6.
Gadomus arcuatus Gilbert and Hubbs, 1920: 392 (in key); Jordan, Evermann and Clark, 1930: 202.

General Characters. Head moderate; 19–22% of total length in complete specimens. Nape high. Trunk fairly long, moderately deep and moderately compressed, tapering gradually into the rather deep, compressed tail; distance from snout to anal fin 36–40% of total length. Greatest depth of body 17–19% of total length. Anus only a short distance (about 10% of head) in advance of origin of anal fin. Abdominal cavity ends at origin of anal fin. About 30 simple, long, slender pyloric caeca.

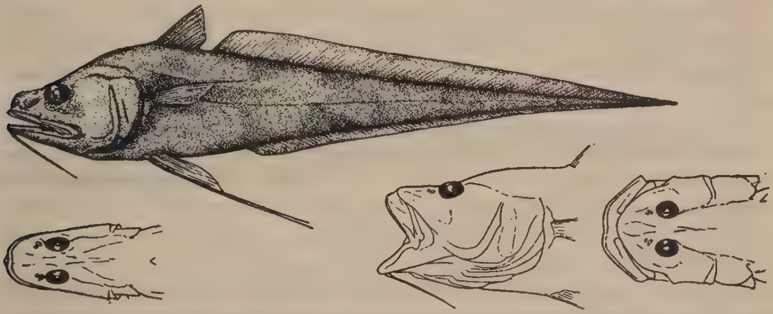

Figure 2.—*Gadomus arcuatus* (Goode and Bean), with side and dorsal views of head with mouth open (on right); dorsal view of head with mouth closed (on left).

Scales. Not seen; about 33 scale pockets on body in a longitudinal series from shoulder over a distance equal to that from snout to dorsal fin. Head scales missing, but entire head, including exposed portion of interoperculum, apparently covered completely. Scales below and before orbits apparently abruptly and conspicuously smaller than those on cheeks behind orbits and on nape and skull above. Ridges on head inconspicuous.

Head Characters. Jaws equal, or lower jaw slightly prominent; cleft of mouth, when closed, only slightly oblique; snout rising steeply backward from upper lip to a moderate height in the anterior mesethmoidal region, behind which the profile follows a long, rather deeply concave curve over the frontal region to the nape (Fig. 2 shows the normal lateral view of the complete fish with deflated gill cavity and closed mouth; the dorsal view of the head is shown below. Dorsal and lateral views of the head from a specimen of the same size with open mouth and distended gill covers are illustrated for comparison). Snout in dorsal view slightly emarginate at tip, barely exposing the point of the lower jaw; length of snout from orbit about 25–30% of head. Mouth large. Upper jaw length about 55% of head. Premaxillaries extend to corner of lips. Barbel thin, but very long, 60–65% of head. Eyes small, lateral; diameter of orbits 17–20% of head. Interorbital space slightly narrower than orbits, 15–16% of head. Preopercle's posterior free margin only very slightly inclined forward of the vertical, forming an angle with the horizontal of about 85°; its lower corner broadly and evenly rounded. Suboperculum only slightly emarginate. The forward part of interoperculum completely hidden in the normal (relaxed) state of the gill cover; posterior portion broadly triangular, exposed and scale-bearing. About 19 short, slender gill rakers on lower limb of first arch, the longest about 5–6% of head; 17 shorter, more club-shaped ones on second arch.

Teeth. Exceedingly minute, in broad ribbons in both jaws.

Fins. Ventrals approximately below origin of dorsal fin, with pectoral fins very slightly in advance. Fins rather short apart from produced rays. 1st dorsal base about 30–35%, its height only about 45%, of head; distance from snout to 1st dorsal fin 15–20% longer than head. Longest rays in 2nd dorsal about 30% of head. Distance from ventrals to anal fin about 75% of length of head. First ray of pectoral fin moderately produced, about 80%, the rest of fin about 60%, of head. Both first and second rays of ventral fin greatly produced, and of approximately the same length, namely about 125–130% of head (incomplete 2nd ray 90%); third ray (normal fin) only about 50% of head.

D_I. 12 V. 8 P. 21–22

General coloration. Dark brown. Oral cavity and gill cavity light dusky, definitely not black, but with variable "cloudy" distribution of pigmentation. Peritoneum black.

Size. Reaches a length of more than two feet.

Range. Known from the Gulf of Mexico and the eastern Atlantic. One specimen, female, 500 mm. long, from "Atlantis" St. 2836.

Gadomus longifilis (Goode and Bean, 1886)

Figure 3.

Bathygadus longifilis Goode and Bean, 1886a: 599; Collett, 1896: 90; Jordan and Evermann, 1898: 2566; Brauer, 1906: 270, pl. XII, fig. 7; Richard, 1910: 149; Murray and Hjort, 1912: 399, fig. 273; Weber, 1913: 173; Roule, 1919: 88; Koefoed, 1927: 116.

Gadomus longifilis Regan, 1903: 459; Gilbert and Hubbs, 1920: 393 (in key); Jordan, Evermann and Clark, 1930: 202; Fowler, 1936: 452, fig. 221.

Hymenocephalus longifilis Vaillant, 1888: 218, pl. XXIII, fig. 1–1c.

General Characters. Head rather small, moderately compressed, 15–18% of total length of complete specimens. Nape not very high. Trunk moderately compressed and moderate in length; distance from snout to anal fin 26–28% of total length. Tail long and very slender. Greatest depth about 12% of total length. Anus only a very short distance in advance of anal fin. Abdominal cavity ends approximately at origin of anal fin. About 10–12 simple, rather short, pyloric caeca.

Scales. About 30 scale pockets in a longitudinal series from the shoulder over a distance equal to that from snout to 1st dorsal fin. Only a few scales of the lateral line present; these are cycloid. Entire head apparently covered (probably not including the narrow exposed margin of interoperculum). Head moderately cavernous, but without strong, externally conspicuous ridges.

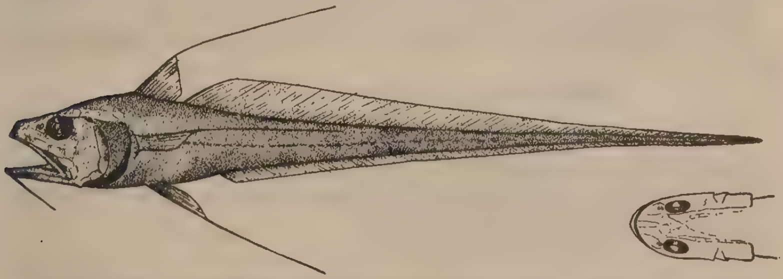

Figure 3.—*Gadomus longifilis* (Goode and Bean), with dorsal view of head.

Head Characters. Profile of head uniformly concave from snout to nape. Snout low, not emarginate at tip; length from orbit 28–30% of head. Mouth large, oblique; lower jaw included when gape is closed.[3] Upper jaws about 60% of head. Premaxillaries extend to corner of lips. Barbel thin, very long, 40–45% of head. Eyes moderate, lateral; diameter of orbit 21–23% of head. Interorbital space 23–25% of head. Posterior free margin of preopercle slightly inclined, forming an angle of about 80° with the horizontal, its lower corner broadly and evenly rounded. Posterior margin of interoperculum exposed, probably not scale-bearing; anterior, major portion completely hidden behind preoperculum. Suboperculum scarcely emarginate. About 28 long, slender gill rakers on lower limb of first arch, the longest about 15% of head; about 21–22 short, slender gill rakers on lower limb of second arch.

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[3] Dorsal view in Fig. 3 with open gape.

Teeth. Exceedingly small, in ribbons in both jaws.

Fins. Pectoral fins inserted approximately below origin of 1st dorsal, the ventrals noticeably behind this vertical. First ray in dorsal, pectoral and ventral fins greatly produced; other rays of these fins rather short. 1st dorsal fin base about 30% of head; distance from snout to dorsal fin only about 5% longer than length of head; first fin ray about twice length of head (200%), second ray only about 40%. Longest rays in 2nd dorsal about 35% of head. Distance from ventrals to anal fin about 60–65% of length of head. Upper pectoral fin ray about 180%, second ray 45–50%, of head. Only first ray in ventral fin produced, 160–170%, second ray about 60%, of head.

D_1. 10[4] V. 8 P. 14–16

General coloration. Uncertain. Oral cavity, gill cavity and peritoneum black.

Size. A small species, probably not exceeding 18 inches in length.

Range. Cosmopolitan in warm regions. One specimen from "Atlantis" St. 2836.

Bathygadus favosus Goode and Bean, 1886

Figure 4.

Bathygadus favosus Goode and Bean, 1886b: 160; 1895: 420, fig. 352; Jordan and Evermann, 1898: 2565; 1900: fig. 908; Gilbert and Hubbs, 1920: 380 (in key); Jordan, Evermann and Clark, 1930: 203.

Bathygadus sp. (*favosus?*) Koefoed, 1927: 114.

General Characters. Head moderate, somewhat cavernous, about 17–20% of total length in complete specimen. Nape fairly low. Trunk fairly long, not deep, relatively little compressed, tapering gradually into the profile of the tail; distance from snout to anal fin about 28–30% of total length. Greatest depth 13–17% of total length. Abdominal cavity ends at origin of anal fin. About 21 simple pyloric caeca.

Scales. Cycloid; about 32–36 scale pockets in a longitudinal series from the shoulder over a distance equal to that from snout to dorsal fin. Head scales mostly lost, but entire head, including exposed part of interoperculum and ventral surfaces of lower jaw, apparently has been completely covered.

Head Characters. Profile of head and nape confluent, only slightly convex; point of snout steep. Snout in dorsal view scarcely emarginate; length from orbits about 29–31% of head. Mouth large; jaws subequal, the lower jaw enclosed, the cleft slightly oblique. Upper jaws 53–60% of head. Premaxillaries extend to corners of lips. Eyes large, lateral; longitudinal diameter of orbits 18–21% of head, or slightly less than ⅔ of the interorbital width, which measures about 31–35% of head. Posterior free margin of preopercle inclined forward

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[4] There is no rudimentary ray in front of the produced dorsal ray in the Bingham Collection specimen.

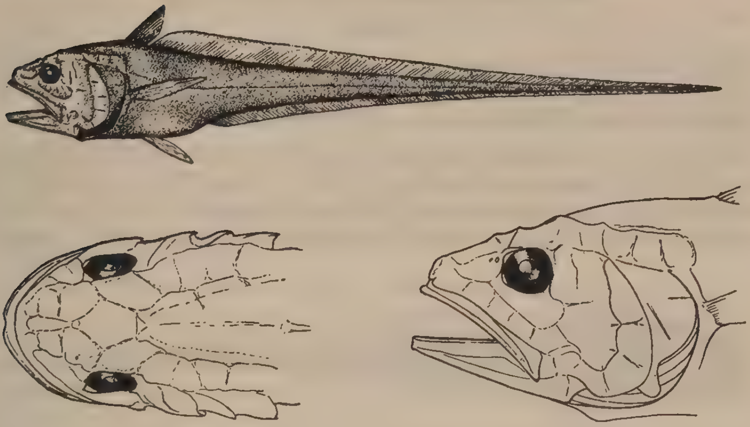

Figure 4.—*Bathygadus favosus* Goode and Bean, with enlarged dorsal and side views of head.

and upward at an angle of about 60° to the horizontal, the lower corner very broadly and evenly rounded. Posterior part of interopercle exposed and scale-bearing. About 20 long, slender gill rakers on lower limb of first arch, the longest about 11–14% of head; 15 short gill rakers on lower limb of second arch.

Teeth. Minute, in broad ribbons in both jaws.

Fins. Insertions of ventrals and pectorals and origin of dorsal fin in a straight line, usually vertical, or with ventrals slightly behind and dorsal slightly in advance of pectorals. Fins moderate, only ventrals with produced ray. 1st dorsal fin base about 25–30%, its height about 50%, of length of head (*fide* Goode and Bean); distance from snout to dorsal fin less than 5% longer than head. Longest rays in 2nd dorsal about 25% of head (*fide* Goode and Bean). Distance from anus to anal fin short, about 10% of length of head, or less; distance from ventrals to anal fin about 60–70% of head. Pectoral fin rays uniformly graduated, the first ray 60–65% of head. Ventral fins probably as in *B. macrops* and *B. vaillanti.*

D. 11 V. 9 P. 14–17

General coloration. Not known with certainty; probably light. Oral cavity, gill cavity and peritoneum dark.

Size. Probably does not exceed a length of two feet.

Range. Known from both sides of the North Atlantic.

Bathygadus vaillanti Roule and Angel, 1933

Figure 5.

Bathygadus vaillanti Roule and Angel, 1933: 63, pl. III, fig. 30; Fowler 1936: 1246, fig. 534.

Bathygadus favosus Hildebrand, in Longley and Hildebrand, 1941: 32.[5]

It is not without hesitation that some specimens from the Gulf of Mexico are being referred to the species described by Roule and Angel from the Azores. In their description and measurements these authors assign to their species two features of which either one might be considered to demonstrate a specific difference from the Mexican Gulf material, but both of which are refuted by Roule and Angel's own illustration and by conflict between figure and text. In their table of measurements Roule and Angel record the length of the snout as only 13 mm., or scarcely more than two-thirds of the diameter of the eye (18 mm.), while the two measurements are equal in our specimens. However, Roule and Angel's illustration also shows length of snout and diameter of eye about equal, and the equality between the length of snout and of the longest rays in second dorsal fin, described by Roule and Angel in their text, also obtains in their illustration. The evidence thus favors the correctness of the figure and not of the table of measurements in regard to the length of the snout. Roule and Angel further state that the ventrals of their specimen are inserted a little in

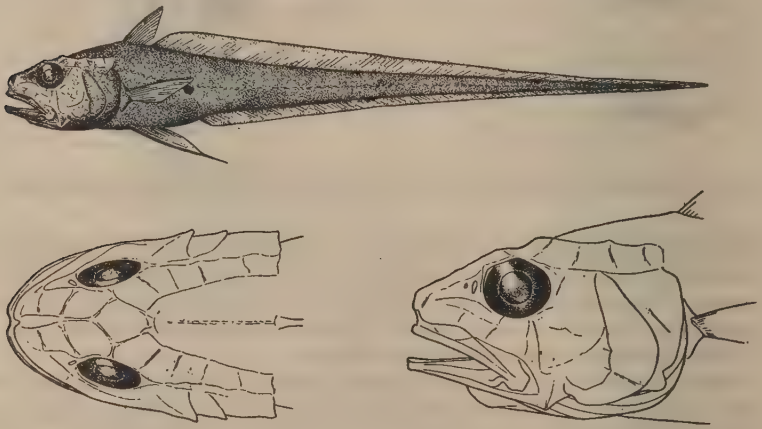

Figure 5.—*Bathygadus vaillanti* Roule and Angel, with enlarged dorsal and side views of head.

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[5] Hildebrand remarks upon the similarity between his specimen and Roule and Angel's account of *B. vaillanti,* but fails to recognize the existence of three separate species in the western Atlantic, referring his own specimen to *B. favosus.*

advance of the origin of the pectorals, but in the figure it is clearly indicated that this is due to the arched pose of the back and will not be true if perpendiculars are drawn to the normal horizontal axis of the body, *i. e.*, to an approximate line from the point of the snout to the mid-height above the origin of the anal fin. Using this interpretation of the figure to correct and supplement Roule and Angel's description, it is impossible to deduce the existence of any significant difference between the Mexican Gulf material and the type specimen. It would be desirable to have this essentially negative identification confirmed or corrected as soon as circumstances may permit. The following is a description of specimens from the Gulf of Mexico.

General Characters. Head moderate, somewhat cavernous, about 17–18% of total length of complete specimen. Nape fairly low. Trunk fairly long, not deep, relatively little compressed, tapering gradually into profile of tail; distance from snout to anal fin about 28–30% of total length. Greatest depth about 13% of total length. Abdominal cavity ends at origin of anal fin. About 28 simple, long, slender pyloric caeca.

Scales. About 32–34 scale pockets in a longitudinal series from shoulder over a distance equal to that from snout to dorsal fin. Scales cycloid. Head scales mostly lost, but entire head, including exposed part of interoperculum and ventral surfaces of lower jaw, apparently has been covered completely.

Head Characters. Profile of head and nape confluent; only slightly convex. Snout in dorsal view scarcely emarginate; point of snout steep; length from orbits about 27–29% of head. Mouth large, its cleft only slightly oblique. Jaws subequal, the lower jaw enclosed. Upper jaws 54–57% of head. Premaxillaries extend to corners of lips. Eyes large, lateral; longitudinal diameter of orbits 24–28% of head. Interorbital width approximately equal to diameter of orbit. Posterior free margin of preopercle inclined forward and upward at an angle of about 55° to the horizontal, the lower corner very broadly and evenly rounded. Posterior part of interopercle exposed and scale-bearing. About 21 long, slender gill rakers on lower limb of first arch, the longest about 14% of head; 19 short gill rakers on lower limb of second arch.

Teeth. Minute, in broad ribbons in both jaws.

Fins. Insertions of ventrals and pectorals and origin of dorsal fin in a straight line, usually vertical, or with ventrals slightly behind and dorsal slightly in advance of pectorals. Fins moderate, only the ventrals with produced rays. 1st dorsal base about 40%, its height 50–55%, of length of head; distance from snout to dorsal fin less than 5% longer than head. Longest rays in 2nd dorsal about 24–27% of head. Distance from anus to anal fin short, about 15% of length of head; distance from ventrals to anal fin about 60–75% of head. Pectoral fin rays uniformly graduated, the first ray 55–60% of head. First ventral ray about 80–85%, second ray 50–55%, of head.

D. 11 V. 8 P. 17

General coloration. Not known with certainty; probably light. Oral cavity, gill cavity and peritoneum dark.

Size. Probably does not exceed a length of two feet.

Range. Known only from the Gulf of Mexico. Two specimens from "Atlantis" St. 2823.

Bathygadus macrops Goode and Bean, 1886

Figure 6.

Bathygadus macrops Goode and Bean, 1886a: 598; Jordan and Evermann, 1898: 2566; Jordan, Evermann and Clark, 1930: 203; Gilbert and Hubbs, 1920: 380 (in key).

General Characters. Head moderate, somewhat cavernous, about 18% of total length of complete specimen. Nape fairly low. Trunk fairly long, not deep; relatively little compressed, tapering gradually into profile of tail; distance from mouth to anal fin about 33% of total length. Greatest depth 13–15% of total length. Abdominal cavity ends at origin of anal fin. About 28 simple, long, slender pyloric caeca.

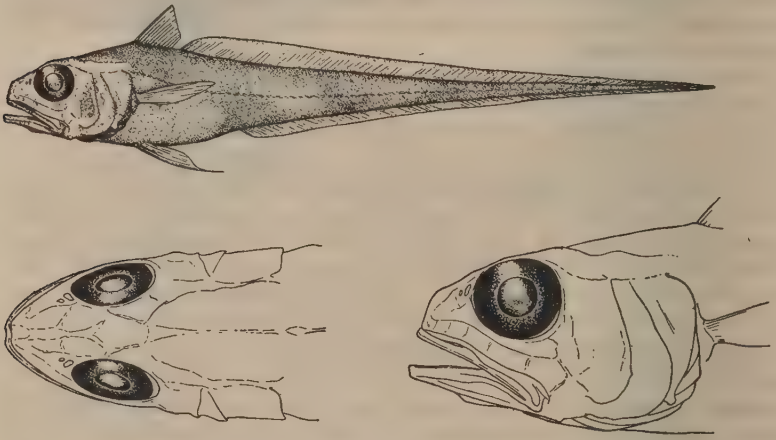

Figure 6.—*Bathygadus macrops* Goode and Bean, with enlarged dorsal and side views of head.

Scales. About 33 scale pockets in a longitudinal series from the shoulder over a distance equal to that from snout to dorsal fin. Scales cycloid. Scales on head mostly lost, but the entire head, including exposed part of interoperculum and ventral surfaces of lower jaw, apparently has been covered completely.

Head Characters. Profile of head and nape confluent, only slightly convex. Snout in dorsal view scarcely emarginate; point of snout steep; length from orbits about 24% of head. Mouth large, its cleft only slightly oblique. Jaws subequal, the lower jaw enclosed. Upper jaws 55–57% of head. Premaxillaries extend to corners of lips. Eyes large, lateral; longitudinal diameter of orbits 32–34% of head. Interorbital width only about ⅔ of orbit, 20–22% of head. Posterior free margin of preopercle inclined forward and upward at an angle of about 75° to the horizontal, the lower corner very broadly and evenly rounded. Posterior part of interopercle exposed and scale bearing. About 19 long, slender gill rakers on lower limb of first arch, the longest about 14–15% of head; 16 short gill rakers on lower limb of second arch.

Teeth. Minute, in broad ribbons in both jaws.

Fins. Insertions of ventrals and pectorals and origin of dorsal fin in a straight line, usually vertical, or with ventrals slightly behind and dorsal slightly in advance of pectorals. Fins moderate; only ventrals with a slightly produced ray. 1st dorsal base approximately equal to its height, or 35% of length of head; distance from snout to dorsal fin less than 5% longer than head. Longest rays in 2nd dorsal about 30% of head. Distance from anus to anal fin short, about 12% of length of head; distance from ventrals to anal fin about 85% of head. Pectoral fin rays uniformly graduated, the first ray 55–65% of head. First ventral ray about 55–72% of head, but only about ⅛ longer than second ray, which is 50–55% of head.

D. 12 V. 8 P. 16

General coloration. Not known with certainty; probably light. Oral cavity, gill cavity and peritoneum dark.

Size. Probably does not exceed a length of 18 inches.

Range. Known from the Gulf of Mexico only.

Subfamily CORYPHAENOIDINAE

In this subfamily it seems desirable to attempt to develop further the basic system laid down by Gilbert and Hubbs. The writer's attention has been given particularly to the genus *Coryphaenoides*, which seems to have been given a far too inclusive interpretation by the above authors.

In their first report, Gilbert and Hubbs (1916: 138) synonymize *Macrourus* with *Coryphaenoides*, claiming that the type of the former, *Macrourus berglax*, is congeneric with the type of the latter, *Coryphaenoides rupestris*. But on the basis of almost every feature which the present writer considers significant, these two species represent opposite extremes and should be generically or subgenerically separated, if any such separations are possible.

Within the group here considered (*Coryphaenoides* Gilbert and Hubbs), we find in *M. berglax* the extreme enlargement and modification of scales along the ridges of head, and extreme reduction of scales in the "naked" areas, both above and below the snout; extreme abbreviation, strengthening and reduction in number of spinules on individual scales; a maximum prominence of snout; maximal distance between ventrals and anal fin; minimal distance between the two dorsals; maximal distinction between the dorso-lateral and ventral surfaces of the head; the first dorsal above or slightly behind the pectoral base; extreme withdrawal of interoperculum under the preopercle.

In *C. rupestris* we find the extreme in uniformity of scales on the head, with no enlarged or reduced scales, no definitely differentiated rows breaking the regular pattern, and no naked areas above or below; extreme production, slenderness and numerousness of spinules on the scales; minimal distance between ventrals and anal fin; the normal long distance between the dorsals; extreme compression of the head, with complete absence of any distinction between latero-dorsal and latero-ventral surfaces; the first dorsal conspicuously in advance of the pectorals; and extreme production of interopercle beyond preopercle.

On the basis of all these features, *Nematonurus goodei*, which was recognized by Gilbert and Hubbs as generically distinct from their *Coryphaenoides* (including *Macrourus*), is certainly much more closely related to *M. berglax* than is *C. rupestris*. Indeed, *N. goodei* would appear to be the closest relative of *M. berglax* among all the western Atlantic forms here considered.

An objection must be made also to Gilbert and Hubbs' cancellation of the genus *Chalinura*, while they retain the genus *Nematonurus*, which they differentiate from their *Coryphaenoides* by the presence of enlarged outer teeth in the premaxillaries, and by a physiognomy usually approaching that of *Bathygadus*. But in *simula*, the type species of *Chalinura*, the physiognomy is entirely that of a Bathygadinae, while this is definitely not true of *goodei*, the type species of *Nematonurus*, since it has a typically macrouroid head; also the outer premaxillary teeth in *Ch. simula* are more conspicuously enlarged than in *N. goodei*. Since the name *Chalinura* (1883) antedates that of *Nematonurus* (1887), the former should have precedence over the latter under the generic definition used by Gilbert and Hubbs, if only one of the two genera were to be retained. In the present report, however, we shall retain both of them under other definitions.

In regard to the genus *Lionurus*, some conflict seems to exist between the features of the genotype and the generic definition given by Gilbert and Hubbs (1916). According to these authors (p. 141), *Lionurus*, in addition to possessing seven branchiostegals, should also be characterized, among other things, by having "anus remote from anal fin; anus preceded by a naked area; . . . Bones of head firm; . . . Scales everywhere well imbricate, their spinules directed backward [with exception of two species]; . . . Snout moderately produced." But according to Günther's description (1887: 141) of the genotype, *L. filicauda*, the snout projects considerably beyond the mouth, and he states explicitly that the bones of the head are soft. In the figure (Günther, 1887: pl. XXXIV B) the anus is indicated immediately in advance of the anal fin.[6] With regard to squamation, the scales in the genus defined by Gilbert and Hubbs are, typically, firmly imbedded and strongly spinulose, while according to Günther's description the scales in the genotype of *Lionurus* are "thin, *cycloid*, and deciduous." Gilbert and Hubbs (1916: 192) recognized a subgenus *Lionurus*, including the genotype, but claimed that the smoothness of the scales was the only distinguishing feature between this subgenus and the subgenus *Nezumia*. But on the basis of the other differences discussed above, it seems evident that the genotype of *Lionurus* cannot be referred to the genus defined by Gilbert and Hubbs; therefore, another designation may have to be found for the latter.

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[6] Confirmed by J. R. Norman *in litt.*

Gilbert and Hubbs (1920: 543 and following) have improved the classification of the species previously listed by them under the generic designation of *Lionurus* by segregating a new genus *Ventrifossa* and by introducing a number of subgenera. The size of the mouth, form of the snout, and features of the gill slit figure prominently in their arrangement of the species into these various systematic units. In the two western Atlantic species there is a striking coincidence between large size of mouth, blunt snout, and short abdomen (*i. e.*, short distance between ventrals and anal fin) while a small mouth and prominent snout are accompanied by a relatively long abdominal distance. According to the measurements given by Gilbert and Hubbs (1916: 193–197), the same relationship between these morphological features also holds for *V. garmani*, the genotype of the large-mouthed genus *Ventrifossa*, and *N. condylura*, the genotype of the small-mouthed genus *Nezumia*. Without complete examination of all the other species, it seems apparent from available illustrations and measurements that this relationship between large mouth and short abdomen expresses a fairly general correlation rather than a specific coincidence. There is also, both in the two western Atlantic species, and in the genotypes of *Ventrifossa* and of *Nezumia*, an equally definite correlation between large mouth and evenly rounded, vertical cheeks[7] and between small mouth and a strong suborbital ridge which divides the scaly upper portion from the naked under side of the head; (Fig. 13 and the description of *Nezumia condylura* given by Jordan, in Jordan and Starks, 1904: 620).

Taking all these correlated features into consideration, it seems reasonable to treat both *Ventrifossa* and *Nezumia* as being of generic rank.

KEY TO THE GENERA OF THE SUBFAMILY CORYPHAENOIDINAE

1a. 2 conspicuous lense-shaped bodies in the mid-ventral line of abdomen, one at the anus and another in the thoracic region before the ventrals, both connected by a line of dark tissue. More than 15 gill rakers on lower limb of second arch. (Scales large, thin and deciduous, weakly ctenoid. Head compressed, cavernous. Mouth large, lateral. Snout short. Branchiostegal rays 7. Anus at anal fin. Dorsal spine smooth. Small delicate species.)
Hymenocephalus sensu stricto, p. 24

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[7] "Cheeks vertical; suborbital area slightly tumid, without definite ridge" in *Ventrifossa garmani*, according to Jordan and Starks (1904: 610).

1b. No lense-shaped bodies on abdomen. Less than 15 gill rakers on lower limb of second arch.

2a. 1st dorsal fin with a long serrate spine.

3a.* Anus in an area of scaleless black skin which is widely separated from origin of anal fin; anal opening itself usually at least about midway between anal fin and ventrals, or nearer to ventrals; an additional scaleless area of black skin, or a forward extension of the area around anus, occurs in some forms. More than 20 pyloric caeca. (Posterior portion and lower margin of interoperculum exposed and scale-bearing. 7 branchiostegal rays. No modified and enlarged scales along base of 2nd dorsal fin.)

4a. Scales very small and delicate, with minute spinules not individually visible to the unaided eye. Rows of scales along each of 4 lower branchiostegal rays. First gill slit almost as long as diameter of orbit; only slightly restricted by a short attachment of lower part of first gill arch to membrane fold. Trunk short and deep; distance from snout to anal fin only about ⅓ longer than head. Origin of anal fin directly below, or immediately behind, vertical from end of 1st dorsal fin base. External color light. Pyloric caeca very numerous, always over 60. (Mouth large and lateral. A separate naked area between anterior ventral fin rays in addition to naked area around anus.) *Malacocephalus*, p. 26

4b. Scales moderate or large, strong, conspicuously spinulose. Branchiostegals and gular region without scales. First gill slit restricted by broad attachment to membrane fold; length of opening ⅓–⅔ diameter of orbit. Trunk not short; distance from snout to anal fin 50–70% longer than head. Origin of anal fin well behind base of 1st dorsal. External color dark. 20–50 pyloric caeca.

5a. Mouth moderate, lateral and subterminal. Upper jaws 2½ or less in head. Snout bluntly rounded, scarcely prominent. No conspicuous suborbital ridge. Head and trunk relatively large, tail moderate. *Ventrifossa*, p. 31

5b. Mouth small, inferior. Upper jaws 3 or more in head. Snout prominent, pointed. Suborbital ridge well defined. Head and trunk small, tail long. .... *Nezumia*, p. 35

3b.† Origin of anal fin at posterior margin of a scaleless area of skin surrounding anal opening, which is thus well separated from base of anal fin. Less than 15 pyloric caeca. (Interoperculum more or less exposed and scale-bearing. Anal fin begins about midway between ventrals and end of abdominal cavity.)

6a. A series of enlarged and modified scales on each side along base of 2nd dorsal fin. Other scales very small, with long erect spinules in irregular quincunx arrangement, giving furry texture. Bones soft. Sensory canals on head greatly developed. Ridges on head not conspicuous externally and without modified scales, but all surfaces of head above mouth completely covered. (Skull with high crests. Head bulky, broad and deep. Tail compressed, rapidly constricted from body)................*Cetonurus*, p. 43

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* Trichotomous; see 3b and 3c.

† Trichotomous; see 3a and 3c.

6b. Scales moderate, without enlarged series along base of 2nd dorsal. Scales with numerous small spinules in subparallel, linear series. Bones firm. Sensory canals on head slightly developed. Suborbital ridge very distinct, with clearly differentiated scales; region below suborbital ridge scaleless anteriorly, nearly to corner of mouth................................*Grenurus*, n. gen., p. 46

3c.* Anus at anal fin, without preceding or surrounding scaleless areas. Pyloric caeca not numerous, about 30 or less. 6 branchiostegal rays.

7a. 2nd dorsal fin with well developed anterior rays of normal size which begin only a short distance behind base of 1st dorsal and far in advance of origin of anal fin. Scales large and strong, scute-like, each with a median, serrate ridge; those on head in several different size-orders, generally not imbricate but separate, the larger scales in definite linear patterns, of which the row along the sharp and complete suborbital ridge, which extends to the preopercle, is most conspicuous; area below snout and suborbital ridge naked; a pair of naked areas behind snout above. Ventral fins below pectorals, without produced ray. Interoperculum entirely hidden behind preoperculum. (About 19 pyloric caeca. Trunk very long, distance from snout to anal fin ⅔ longer than head, distance from outer ventral rays to anal fin less than 1.5 in head. Snout prominent, pointed.)...................*Macrourus*, p. 50

7b. 2nd dorsal fin with reduced anterior rays beginning well behind origin of anal fin. Scales not scute-like, those on head imbricate; suborbital ridge more or less incomplete. First ventral fin ray always conspicuously produced. Interoperculum exposed beyond preoperculum posteriorly.

8a. Trunk very long; distance from snout to anal fin nearly twice length of head; ventrals well behind pectorals, but distance from base of outer ventral rays to anal fin more than ⅔ length of head. (Scales uniformly spiny on all parts of body, with spinules arranged in regular series. Snout low, prominent. Mouth moderate or small. Pyloric caeca few, 10–12.)
Nematonurus, p. 53

8b. Trunk moderate or short; distance from snout to anal fin less than ⅔ longer than head; distance from outer rays of ventral fin to origin of anal less than ⅗ length of head.

9a. Distance from outer ventral rays to origin of anal less than ⅗, but more than ⅖, of length of head. Distance from snout to anal fin less than ⅔, but more than ⅓, longer than head. Exposed portion of interoperculum not encased in a separate fleshy flap, but joined with lower corner of suboperculum under a continuous or only slightly indented dermal edge. Pyloric caeca few, 6–15.

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* Trichotomous, see 3a and 3b.

10a. Scales adherent; strongly and uniformly spinigerous on all parts of body. Spinules not in series, but in irregular quincunx, or without definable pattern in their arrangement on scales. Lower and upper surfaces of snout completely scaly. Eyes large, less than 4 in head. Mouth moderate or small. Upper jaws about 3 in head. Exposed posterior corner of interoperculum wide and strong. *Cariburus*, n. gen., p. 57

10b. Scales easily lost; those on back and tail distinctly to very strongly spinigerous, those on lower flanks and belly often less ctenoid. Spinules, when present, arranged in very regular rows on each scale, giving characteristic striated texture. Lower surface of snout scaleless; a scaleless area on each side above, and immediately behind, the frontolateral edge of snout, which carries a well marked linear row of adherent scales. Eyes small, more than 4 in head. Mouth moderate or large; 2.5 or less in head. Exposed posterior end of interoperculum in the form only of a thin and narrow, greatly produced and attenuate corner, which meets with the lower corner of suboperculum to support jointly a well marked and prominent corner in the dermal margin of outer gill cover. . .*Chalinura*, p. 64

9b. Distance from outer ventral rays to origin of anal fin about 5 or more in head. Distance from snout to anal fin only ⅛ or less longer than head. Exposed portion of interoperculum does not meet suboperculum under the skin, but projects independently in a separate fleshy flap. About 30 pyloric caeca. (Head deep, compressed. Cheeks flat. Squamation on head complete and uniform,[8] extending uninterrupted to the upper lip without naked areas either above or below the snout. Spinules on scales numerous, diffusely scattered or in irregular quincunx, very long and almost erect, giving a furry texture. Eyes large, less than 4 in head. Snout very high, moderately prominent.) *Coryphaenoides*, p. 74

2b. 1st dorsal spine smooth.

11a. Scales very small. Anal opening remote from anal fin, either in, or preceded by, a naked mid-ventral area. Snout blunt, only slightly prominent. 7 branchiostegal rays. Head uniformly covered, with no naked areas anteriorly, either above or below snout; head without conspicuous ridges or modified rows of scales.

12a. Anus in an oval naked area behind ventrals and preceded by a separate naked area farther forward, between, or anterior to, ventral fin bases.

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[8] Except with regard to gradual variations in the size of scales in different regions.

Each small scale with numerous minute spinules in irregular quincunx order, giving a finely diffuse texture to the outer surface. Pyloric caeca numerous and profusely branched (more than 60 ultimate branches). Premaxillary teeth in 2 series, those of outer series conspicuously enlarged. Scales on gill membranes in rows along branchiostegal rays. (Interoperculum extends beyond preoperculum, its exposed portion with scales.)..................*Malacocephalus*, p. 26

12b. Anus in a relatively broad naked area extending from the bases of posterior ventral rays to anal fin; no separate naked area farther forward. Each minute scale with a moderate number of long, erect spinules, giving the external surface a coarsely furry appearance. Pyloric caeca few and simple, less than 20 ultimate diverticles. Premaxillary teeth in a band. Scales on gill membrane in a row or band along inner edge of hyoids. (Small species.)................*Trachonurus*, p. 78

11b. Scales moderate or large. Anus at origin of anal fin without naked area; separate naked area between ventrals present or absent. Snout prominent, pointed, sometimes greatly produced; mouth small, inferior. 6 branchiostegal rays. Dorso-lateral surface of head separated from latero-ventral surface by a prominent suborbital ridge extending from the point of snout to the angle of preopercle and armed with a row of modified scales; other ridges, and rows of modified scales, usually present also. 10–20 pyloric caeca. Interoperculum does not extend to edge of preoperculum, its posterior portion being completely hidden behind the latter and widely separated from suboperculum. Posterior margin of suboperculum with a wide emargination, in which the upper branchiostegal is exposed and enters into the formations of outer gill cover.

13a. A scaleless black area between, or anterior to, bases of ventral fins. Ventral area between mouth and suborbital ridge scaly, with the exception of a narrow median line in front below tip of snout. Snout moderately produced, its length from orbits more than 2½ in head. Each scale with numerous separate and subequal spinules, giving a uniform surface texture. Lower limb of suboperculum in the form of a wide, broadly rounded lamella, its margin not free, but continuous with the edge of the upper branchiostegal.
Coelorhynchus, p. 82

13b. No scaleless areas on ventral surface of abdomen. Entire ventral surface of head below snout and suborbital ridge naked. Snout extremely long, its length from orbit less than 2½ in head. Each scale with a middle horizontal series of closely packed enlarged spinules, appearing as a sharp keel which increases in height posteriorly; smaller spinules form minor and less conspicuous secondary keels on larger scales. Lower limb of suboperculum produced into a long tapering extension, which projects as a free flap overlapping the branchiostegal rays in a downward and backward direction.
Oxygadus, p. 88

Genus **HYMENOCEPHALUS** Giglioli, 1884

Hymenocephalus Giglioli, 1884: 228.[8a]
Mystaconurus Günther, 1887: 139.

Head large and deep.[9] Branchiostegal rays 7. Trunk short; distance from snout to anal fin less than ⅔ longer than head. Tail long; about 70% of total length, or more. Two conspicuous lense-shaped bodies in mid-ventral line, one at anus and the other in thoracic region before bases of ventrals, with a line of dark tissue between the two bodies. Anus at origin of anal fin. Pyloric caeca in moderate numbers (10–15). Scales delicate, fairly large, very deciduous, weakly ctenoid. No modified scute at point of snout. Snout high, but only slightly prominent. Mouth large, lateral. More than 15 gill rakers on lower limb of second arch.[9] Eyes large.[9] Posterior margin of preopercle vertical or only slightly inclined. Cheeks not oblique. Dorsal spine smooth.[9] Origin of 2nd dorsal well behind origin of anal fin, the anterior rays of former greatly reduced. Origin of anal fin at end of abdominal cavity, its distance from anterior end of ventral fin bases approximately half the length of head. Ventral fins usually with 10–11 rays.

Gilbert and Hubbs (1920) introduce two new subgenera, *Hymenogadus* and *Papyrocephalus*, by the inclusion of which they broaden the definition of the genus *Hymenocephalus* sensu lato to the point where its diagnosis rests almost entirely upon the lense-shaped bodies. The writer is inclined to believe that the elevation of the two subgenera to generic rank might prove justifiable and advantageous, but since such a move would be beyond the scope of the present report he has confined himself to the use of the generic designation in its strictest sense, leaving the status of *Hymenogadus* and *Papyrocephalus* out of consideration.

Hymenocephalus cavernosus (Goode and Bean, 1886)

Figures 7, 24 (p. 77).

Bathygadus cavernosus Goode and Bean, 1886a: 598; Günther, 1887: 156.
Hymenocephalus cavernosus, Goode and Bean, 1895: 408, fig. 341; Jordan and Evermann, 1898: 2580; 1900: fig. 912; Jordan, Evermann and Clark, 1930: 207.

General Characters. Head large and cavernous; length about 17–18% of total length of complete specimen. Trunk short; distance from snout to anal fin about 28–29% of total length of complete specimen, or 160% of head. Tail thin and whip-like. Greatest depth about 75–80% of head, 14% of total length. Mid-ventral region with two apparently luminous organs connected with each other by a streak of dark pigmentation; each organ consists of a whitish opaque circular body surrounded by black tissue; anterior organ situated in thoracic

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[8a] Original reference not seen.

[9] These characters are valid only for the genus *Hymenocephalus* sensu stricto or subgenus *Hymenocephalus* of Gilbert and Hubbs (1920); see discussion above.

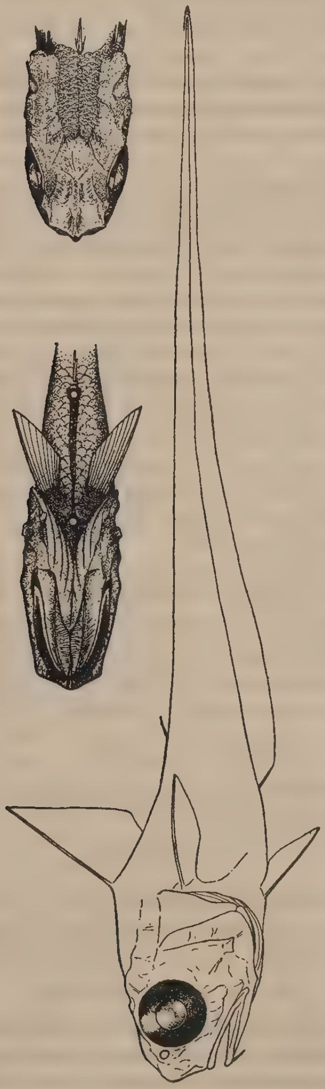

Figure 7.—*Hymenocephalus cavernosus* (Goode and Bean), with ventral view of head and anal region, as well as dorsal view of head.

region well in advance of bases of ventrals, the posterior organ at anus. Abdominal cavity extending to origin of anal fin. 13 short, thick, simple pyloric caeca.

Scales. Very deciduous, variously reported to be cycloid or ctenoid on body in general; small scales in thoracic region definitely ctenoid; pockets rather large, except on nape and in thoracic region; counts not obtainable. No information about scales on head.

Head Characters. Snout high and steep, its point barely extending beyond mouth, the angle of inclination of its ventral profile about 75°; length from orbits about 25%, height from point of snout to mouth about 18%, of head. Mouth relatively large, lateral, subterminal. Upper jaws about 56% of head. Barbel hair-fine, but fairly long, about 14–15% of head. Eyes large, lateral, subcircular; diameter of orbits about 36–37% of head; upper margins of orbits not indented in lateral outlines of top of skull. Interorbital width about equal to diameter of orbits. Angle of inclination of preoperculum's posterior free margin about 70°; its lower corner evenly rounded; outer lamella at its lower end produced into a roughly rectangular free flap with pointed corners. Suboperculum moderately emarginate, its lower corner rounded. Interoperculum slightly exposed beyond preoperculum below and posteriorly, where it is contiguous with suboperculum. About 18–20 gill rakers on lower limb of second arch.

Teeth. Minute, in bands in both jaws.

Fins. Origins of 1st dorsal, pectoral, and ventral fins approximately above each other in a nearly vertical line. 1st dorsal fin fairly large, its height about 70%, its base about 33%, of head; snout to 1st dorsal less than 10% longer than head. Anterior rays of 2nd dorsal minute. Distance from anterior end of base of ventrals to origin of anal fin relatively long, 50–55% of head; length of pectorals about 60%, ventrals about 45–50%, of head.

D_{I}. 12   V. 11   P. 11

General coloration. Probably light silvery; pale in preservative.

Size. Less than one foot in length.

Range. Known only from the Gulf of Mexico.

Genus **MALACOCEPHALUS** Günther, 1862

Malacocephalus Günther, 1862: 396; Lilljeborg, 1891, *2:* 273; Goode and Bean, 1895: 414; Gilbert and Hubbs, 1916: 141 (in key), 189; 1920: 541; Weber and Beaufort, 1929: 61.

Head relatively large. 7 branchiostegal rays. One transverse scaleless fossa between, or slightly anterior to, bases of ventrals, entirely separate from a second scaleless area which precedes or surrounds anus. Pyloric caeca very numerous and profusely branched, with 80–200 ultimate diverticles. Scales small, with minute spinules. Head externally smooth, with a uniform and complete squamation on all outer surfaces except those of gular and branchiostegal membranes, where scales may be present or absent; no scaleless areas above or below on snout; no distinct scute at tip of snout. Mouth large, lateral, upper jaws more than 40% of length of head. Gill slit wide. Less than 15 gill rakers on lower limb of second arch. Eyes moderate, lateral. Free margin of preoperculum approximately vertical. Dorsal spine serrate or smooth. Anterior rays of 2nd dorsal minute. Pectorals very high on sides. Ventrals small, with 8–9 rays. Distance between ventrals and anal fin very short, less than ⅓ of length of head, with the origin of anal fin below, or anterior to, end of base of 1st dorsal.

The genus as a whole consists of the genotype on one hand and a small group of species on the other, all of which have certain significant differences from the genotype in common. Subgeneric distinctions therefore seem both practicable and desirable, and a new subgenus is introduced herewith.

KEY TO THE SUBGENERA OF MALACOCEPHALUS

1a. Branchiostegal membranes without scales. Anus at posterior end of second scaleless fossa. Dorsal spine smooth. Teeth in single series in lower jaw, 2 series in premaxillaries. . . . . *Malacocephalus*, below

1b. Branchiostegal membranes with scales in rows at least along 4 lower branchiostegal rays. Anus approximately in center of second scaleless area below. Dorsal spine serrate or smooth. Dentition variable. *Pawnurus* n. subgen., below

Subgenus **MALACOCEPHALUS** Günther

Characters as listed in the preceding key. A re-examination of the species to compare it in greater detail with those of the subgenus *Pawnurus* would be very desirable, but conditions of war unfortunately make it impossible to obtain the required samples at the present time.

So far as one can judge from the literature the subgenus contains only the genotype *M. laevis* (Lowe). Describing material from the East Indies, Weber and Beaufort (1929: 63) specifically mention the subgeneric characters, thus at least demonstrating the very wide range of the subgenus as a whole, whether or not it should subsequently prove possible to distinguish several species. In the Atlantic *M. laevis* ranges very widely in the east, from Scandinavia to South Africa, although it has not been recorded as yet from the western North Atlantic and has been reported only once from the western South Atlantic off Pernambuco, Brazil (Günther, 1887: 148).

PAWNURUS, new subgenus

Type species: *Malacocephalus occidentalis* Goode and Bean.

Distinguished from the subgenus *Malacocephalus* by the presence of scales on the branchiostegal membranes in rows along the branchiostegal rays, and by having the anus surrounded by, rather than preceded by, the second scaleless fossa on the ventral surface.

In the type species we also find the posterior corner and lower margin of the interoperculum exposed and scale-bearing; the origin of the anal fin about midway between the bases of the ventrals and the end of the abdominal cavity. Due to inadequate information about the genotype, it is impossible to tell whether these and other features which could be added to the subgeneric diagnosis are actually of only subgeneric or of generic significance.

With the exception of the material referred to *Malacocephalus laevis*, it seems indicated that all of the Pacific species belong to the subgenus *Pawnurus*. The Atlantic *M.* (*Pawnurus*) *occidentalis* differs from the Pacific species by its serrate dorsal spine and by the inner band of teeth in its upper jaw.

Malacocephalus (Pawnurus) occidentalis Goode and Bean, 1886

Figures 8, 9 (p. 31).

Malacocephalus occidentalis Goode and Bean, 1886a: 597; 1895: 415; Jordan and Evermann, 1898: 2570.

Chalinura occidentalis Jordan, Evermann and Clark, 1930: 204; Hildebrand, in Longley and Hildebrand, 1941: 32; Vladykov and McKenzie, 1935: 66.

General Characters. Head small, scarcely compressed; about 16% of total length of complete specimens. Trunk short and deep, scarcely compressed; distance from snout to anal fin about 20–22% of total length, only 30–35% longer than head. Tail long, slender and compressed. Greatest depth only slightly less than length of head. Anal opening much nearer to bases of ventral fins than to origin of anal fin, its distance from the latter being about 50–60% of the distance between anterior end of ventral fin bases and origin of anal. Anus surrounded by a circular naked area beginning immediately behind a line connecting posterior ends of ventral fin bases; a second separate transverse naked area in the form of a minor segment of a circle with the arc directed forward occurs between anterior ends of ventral fin bases. Abdominal cavity rather deep, extending beyond origin of anal fin for a distance equal to about 25% of length of head. About 82 slender pyloric caeca reckoned by distal count.

Scales. Body scales small and delicate, each scale with about 20–30 minute spines; about 65–75 scales in a longitudinal series from the shoulder over a distance equal to that from snout to origin of 1st dorsal fin. Squamation of head unusually complete, with no naked areas above or below snout; bands of scales along each of the 4 lower branchiostegal rays on each side; exposed portions of interoperculum also completely covered with minute scales, as are also the lower surfaces of the rami of the lower jaw, except at their anterior ends; scales on head show no conspicuous pattern or individual modification, except for a reduction to almost rudimentary size below the point of snout. Head without external ridges, but with a fairly high subdermal crest in the median of snout from between eyes to rostral lamellae.

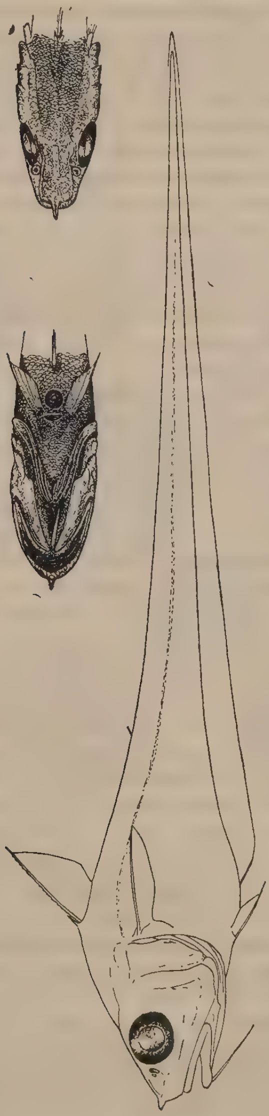

Figure 8.—*Malacocephalus (Pawnurus) occidentalis* Goode and Bean, with ventral and dorsal views of head.

Head Characters. Snout length from orbits about 23–26%, its height about 13%, of head. Dorsal profile of head and nape rises quite steeply towards the rather high elevation of the anterior part of the back carrying the 1st dorsal fin. In the completely undamaged state the snout is distinguished by the unicorn-like projection of a pair of rostral lamellae. These lamellae probably represent extensions of the nasals, continuing a rather high but entirely subdermal anterior crest of the frontals. This crest begins approximately above the centers of the eyes. The two lamellae are closely applied to each other, giving the appearance of a single projection, which, in life and in the smaller specimen, is covered by continuous skin as suggested in Fig. 8. But even in the exceptionally well-preserved larger specimen the lamellae have pierced the skin, and their transparent plates are bent over so as to be easily overlooked. This will probably be the usual state of museum specimens, in which case the profile of the snout appears only very slightly prominent, and the entire side view of the head seems definitely more "gadoid" than "macrouroid." The projecting lamellae are about equal to half the height of the snout. Apart from the rostral projection, the snout in dorsal view is rather squarely truncated, but not very wide. Mouth relatively large, lateral, subterminal. Upper jaw nearly half (47–48%) of length of head. Premaxillaries extend the full length of opening of mouth, which reaches well beyond centers of eyes. Barbel long and thin, 40% of head. Eyes large, lateral, slightly elliptical; longitudinal diameter of orbits about 28–30% of head; upper margins of orbits barely curved in dorsal view. Interorbital space fairly wide, 1.4 in orbit, 20–22% of head. Preopercle's posterior free margin rises almost vertically or slightly inclined forward, its lower corner distinctly arched backward, but broadly rounded. Posterior upper margin of subopercle also vertical or slightly inclined forward, its posterior lower margin barely concave. Posterior and lower portions of interoperculum exposed beyond preoperculum throughout its entire length. Upper branchiostegal ray completely hidden. First gill slit rather wide, its length 30% of the length of head. 8–9 short gill rakers on lower limb of second arch.

Teeth. A broad, scattered band of minute teeth in upper jaw, with a single outer series of very wide-set enlarged teeth (only about 10 in each premaxillary). Lower jaw with a single series of teeth of medium size.

Fins. Moderate. 1st dorsal origin conspicuously, but not very far, behind origin of pectorals, with ventrals approximately below pectorals. 1st dorsal base about 28–30%, its height about 65%, of head; distance from snout to 1st dorsal fin about 20% longer than head. 2nd dorsal origin far behind origin of anal, which is barely behind the vertical from end of base of 1st dorsal; anterior rays of 2nd dorsal rudimentary. Distance from anal fin to anterior end of ventral fin bases short, only about 30% of length of head. Pectorals high, their length about 60% of head. Slightly produced ventral ray about 38–40% of head.

D_1. 13 V. 8 P. about 18

Coloration. General external coloration very light, but with a dark distal area over the middle rays of first dorsal; dark ventrals; dark pectoral axil, but light pectorals, and a dark distal spot in the anterior part of the anal (not well defined). Naked areas black. Jaws, lips and proximal part of barbel dark. Branchiostegal membranes dark inside and outside, but gill cavity and mouth light.

Size. Does not exceed a length of one foot.

Range. Tropical and subtropical eastern North Atlantic. One specimen from "Atlantis" St. 2817.

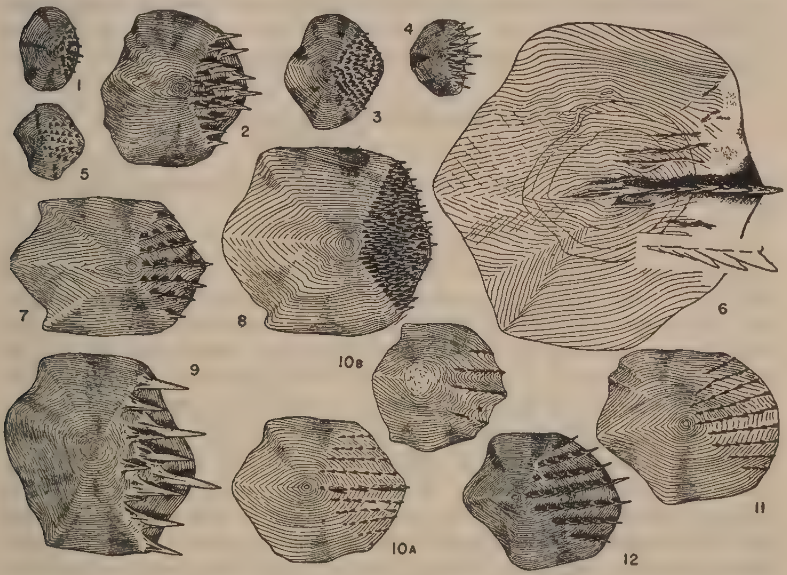

Figure 9.—Enlarged drawings (× 25) of scales from flanks of: (1) *Malacocephalus (Pawnurus) occidentalis;* (2) *Ventrifossa atlantica*, n. sp.; (3) *Nezumia bairdii;* (4) *Cetonurus globiceps;* (5) *Grenurus grenadae*, n. sp.; (6) *Macrourus berglax;* (7) *Nematonurus armatus;* (8) *Cariburus zaniophorus;* (9) *C. mexicanus*, n. sp.; (10) *Chalinura simula;* (11) *C. carapina;* (12) *C. brevibarbis.*

Genus **VENTRIFOSSA** Gilbert and Hubbs, 1920

Ventrifossa Gilbert and Hubbs, 1920: 543; Barnard, 1925: 345; Weber and Beaufort, 1929: 64.

Head rather smooth. Branchiostegal rays 7. No lense-shaped luminous organs. Anus in a rounded scaleless area which begins between, or immediately behind, bases of ventrals and ends far in advance of origin of anal fin. 20-50 pyloric caeca. No enlarged scales along base of 2nd dorsal fin. Spinules on scales do not form regular linear series, but may be found in irregular rows or in irregular quincunx order. Snout short. Mouth wide, length of upper jaws at least 40% of length of head. First gill slit restricted. Less than 15 gill rakers on lower limb of second arch. Eyes lateral, moderate or large. Suborbital ridge rounded, externally inconspicuous. Interoperculum partly exposed and scale-bearing. Teeth in bands in both jaws, the outer series in upper jaw often enlarged. Dorsal spine serrate.

The writer is not entirely convinced that it is actually satisfactory to refer the new Atlantic species herein described to the Pacific genus *Ventrifossa*. The type of the genotype, *garmani*, is rather shrunken and therefore comparisons are difficult on several points. Re-examination of the type species on the basis of new material would be very desirable, and might possibly lead to a subdivision of the genus.

Ventrifossa atlantica, new species

Figures 10, 9 (p. 31).

Type specimen, B.O.C. No. 2103; "Atlantis" Station 2836, in the Gulf of Mexico.

General Characters. Head not compressed; there is no complete specimen available, but it seems indicated that the head would be contained about 6 times in the total length of an undamaged fish (5 times in length of specimens with last part of tail missing). Trunk fairly long, moderately compressed; distance from snout to origin of anal fin about 50% longer than head. Tail moderately compressed, the trunk and tail evenly graduated into each other. Greatest depth about 85% of head. The abdominal cavity, which is rather deep and capacious posteriorly, extends beyond origin of anal fin for a distance equal to about 18% of length of head. Rather large and wide naked area of simple oval contour surrounding anus, with its anterior end extending only very slightly forward between posterior parts of ventral fin bases; length of naked area equals about 18–20% of length of head. Rather prominent papilla behind the anal opening. About 37–38 long, slender pyloric caeca (reckoned by distal count) arising from a lower number of proximal diverticula, each of which generally divides twice very near base.

Body Scales. Moderate, firmly adherent, with about 20–30 long spines in roughly parallel, but rather irregular, rows, producing a furry texture; about 44 in a longitudinal series from shoulder over a distance equal to that from snout to 1st dorsal fin.

Head Scales. Squamation on neck joins that on top of head without any abrupt change in size or arrangement of scales; normal scales absent in anterior area between point of snout and mouth, the skin in this region largely naked or provided only with irregularly scattered rudimentary scales; entire head otherwise very uniformly covered with moderate-sized, very spiniferous scales having their spinules arranged in radiating rows which produce a very characteristic texture; this squamation also covers entire outer gill cover, including exposed

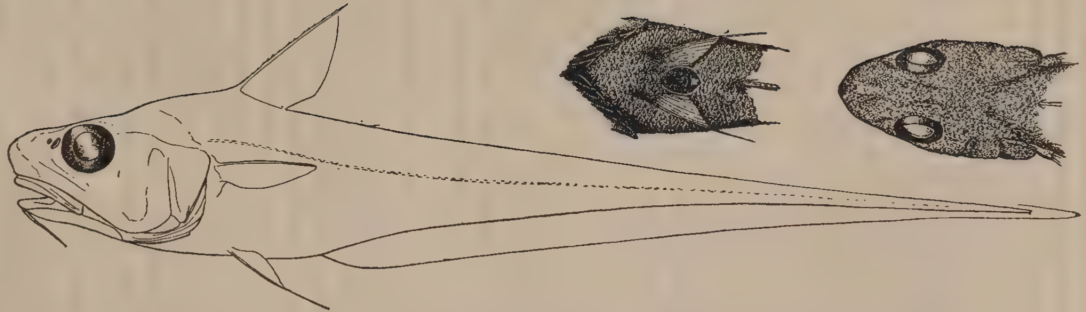

Figure 10.—*Ventrifossa atlantica*, n. sp., with ventral view of anal area and dorsal view of head.

part of interoperculum and ventral surfaces of rami of lower jaw. Branchiostegal membranes and gular region scaleless. Head without externally conspicuous ridges. Scales rigidly attached along orbital rims and in a series between orbit and upper jaw, but not fixed to upper surface of skull. Point of snout without clearly differentiated shield.

Head Characters. Snout bluntly rounded both in lateral and dorsal view, but of only moderate height and width, its lower profile rising almost perpendicularly from mouth, or with a slight forward inclination; sides of snout, in horizontal view from above, converging anteriorly at a bluntly rounded angle of about 120°; length of snout from orbits about 28–30%, median ventral length (height) of snout from mouth about 15–16%, of head. Mouth relatively large. Upper jaw length about 42% of head. Premaxillaries extend very nearly to corner of mouth. Barbel slender but fairly long, about 30% of head. Eyes moderate, subcircular, essentially lateral; diameter of orbits 27–28% of head; upper margins of orbits only shallowly indented in lateral outlines of top of head, as viewed from above. Interorbital width moderate, 1.2–1.3 in orbit, about 21% of head. Preopercle's posterior free margin rises almost vertically, its lower corner broadly rounded. Posterior margin of the rather broad suboperculum gently convex in general, with a barely perceptible concavity in its lower third. Interoperculum relatively large; its wide posterior portion extends well beyond preoperculum and is broadly adnate to lower margin of suboperculum. Upper branchiostegal ray completely hidden. First gill slit about 20% of length of head. 8 short, tubercular gill rakers on lower limb of second arch.

Teeth. In both jaws in broad bands, with an outer series of conspicuously enlarged teeth in upper jaw.

Fins. Moderate. Bases of pectoral fins slightly in advance of ventrals, which are below, or slightly anterior to, origin of 1st dorsal fin. 1st dorsal base about 27–28%, its height (including filamentous tip) about 70%, of length of head; snout to 1st dorsal fin about 15% longer than head. 2nd dorsal origin far behind origin of anal fin, which is well behind end of base of 1st dorsal. Length of pectorals about 50%, the moderately produced first ventral ray about 55–60%, of head. Distance from anterior end of ventral fin base to origin of anal fin rather long, about 45% of length of head. Anterior rays of 2nd dorsal fin small but well defined. Origin of anal fin in last third of distance from ventrals to end of abdominal cavity. Distance from anal opening to anterior end of base of ventrals only ½–⅔ of distance from anus to anal fin.

D_{I}. 12 V. 10 P. about 23

General coloration. Deep brownish black. Oral and branchial cavities also black. Peritoneum and intestines light.

Size. Length about 15 inches.

Range. Gulf of Mexico. One specimen from "Atlantis" St. 2836, and one from "Atlantis" St. 2853 T.

Genus **NEZUMIA** Jordan, 1904

Nezumia Jordan, in Jordan and Starks, 1904: 620.
Nezumia (subgenus of *Lionurus*) Gilbert and Hubbs, 1916: 145, 193; 1920: 553, 554.

Branchiostegal rays 7. Abdomen not shortened; distance from snout to anal fin 50–70% longer than head. Anus far in advance of anal fin, surrounded by an area of scaleless black skin (with a forward extension in western Atlantic species; a separate anterior scaleless area between ventrals in genotype). No lense-shaped luminous organs. 20–40 pyloric caeca.[10] Scales ctenoid, with subequal or only slightly differentiated spinules; no modified or enlarged scales along base of 2nd dorsal. Point of snout without clearly differentiated terminal scute. Snout prominent, pointed. Suborbital ridge weakly to moderately developed. First gill slit restricted. Less than 15 gill rakers on lower limb of second arch. Eyes moderate to large; diameter of orbits about ⅓ of length of head.[11] Posterior portion of interoperculum exposed and scale-bearing.[10] Teeth in cardiform bands in both jaws, without conspicuously enlarged series, although slight differentiations occur between outer and inner teeth. Dorsal spine serrate. Anterior rays of 2nd dorsal fin rudimentary. Origin of anal fin in middle fifth of distance between ventral fins and end of abdominal cavity.

The western Atlantic form, *N. bairdii*, was first assigned to the subgenus *Nezumia* by Gilbert and Hubbs (1916: 145), who reject the use of the number of rays in the ventral as the differentiating character of the subgenus (*loc. cit.:* 193). Instead they define it by the ctenoid nature of its scales, while crediting cycloid scales to the subgenus *Lionurus*. The writer agrees entirely in this assignment of *N. bairdii*, and in the opinion that the number of ventral fin rays is not a critical generic character, although very useful when it shows a narrow range of variation within a genus which is defined by other and more significant features. In *Nezumia*, as interpreted by Gilbert and Hubbs and by the present writer, the range of variation in ventral fin count is from 5 to 17, with 7 being counted in *N. bairdii*, and 14 to 17 in the genotype.

As a basis for the relegation of *Lionurus* and *Nezumia* to subgeneric ranks, Gilbert and Hubbs make the statement that the species grouped in the subgenus *Lionurus* are distinct from those referred to *Nezumia* only by the smooth scales (Gilbert and Hubbs, 1916: 192). But in so stating, these authors failed to take the characters of the actual genotype of *Lionurus* (*L. filicauda*) into account. This is a *lapsus calami* probably related to the fact that the genotype was the only species assigned by them to the subgenus *Lionurus*, which they had not had opportunity to examine.[12] Günther's figure and description show quite clearly, however, that the difference between the genotype of *Lionurus* and the species of *Nezumia* is even greater and more significant than the differences between *Nezumia* and *Ventrifossa* (see p. 18). Thus *Nezumia* cannot be a subgenus of *Lionurus*, or of any other genus of earlier introduction, and therefore automatically assumes generic rank, while the status of the genus *Lionurus* becomes somewhat unclear but beyond the scope of the present report.

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[10] Valid for genotype *N. condylura* Jordan and Gilbert, *fide* Gilbert and Hubbs, 1916: 196 (24–36 caeca) and for the western Atlantic species. Not verified throughout genus.

[11] In genotype as well as in western Atlantic species.

In their list of species, Gilbert and Hubbs (1916: 145) also include in *Nezumia* Goode and Bean's *Malacocephalus occidentalis*, but it seems evident (see p. 27) that there was far greater justification for the original classification of this species, although it still remains a difficult choice whether to include it in the genus *Malacocephalus*, or in a separate but closely related genus of its own.

KEY TO THE SPECIES OF *Nezumia*

1a. Only 7 rays in ventral fins. Spinules on scales narrow (see Fig. 11)..*bairdii*, p. 37
1b. Ventral fins with 9 rays. Spinules on scales broad, formed like short, double-edged swords, and so arranged as to give the appearance of an imbricate cover on the scale..*hildebrandi*, n. sp., p. 40

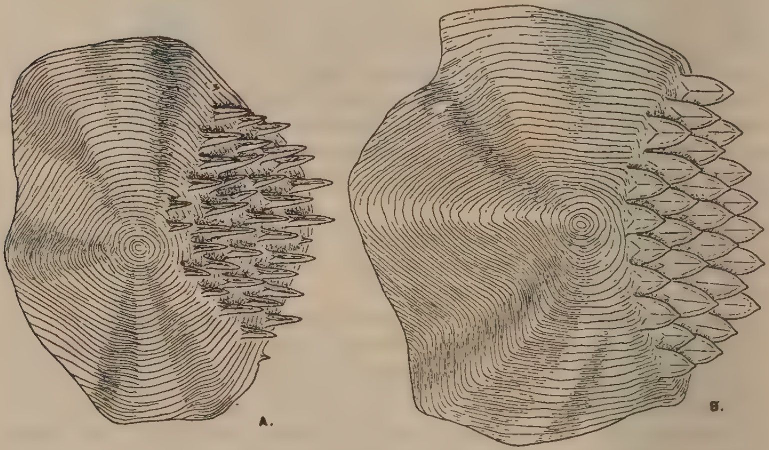

Figure 11.—Enlarged drawings of scales from flanks of: (A) *Nezumia bairdii* (Goode and Bean); (B) *N. hildebrandi*, n. sp.; × 48.

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[12] See the list of species in Gilbert and Hubbs, 1916; 145.

Nezumia bairdii (Goode and Bean, 1877)

Figures 12, 9 (p. 31).

Macrurus[13] *bairdii*[14] Goode and Bean, 1877: 471; 1880: 7; 1883: 195; 1895: 393, fig. 335; Goode, 1881: 337, 475; Günther, 1887: 135, pl. XXXII, fig. B; Jordan and Evermann, 1898: 2583; Smith, 1898: 107; Linton, 1898: 517; 1901b: 480; Howe, 1901: 240; Brauer, 1906: 389; Kendall, 1908: 145; Sumner, Osburn and Cole, 1913: 771; Wilson, 1920: 579; 1932: 506, 528; Bigelow and Welsh, 1925: 468, fig. 235; Nichols and Breder, 1927: 174; Borodin, 1928: 13; Breder, 1929: 287, fig.; Jordan, Evermann and Clark, 1930: 205; Firth, 1931: 13; Roule and Angel, 1933: 59; Vladykov and Tremblay, 1935: 82; Vladykov and McKenzie, 1935: 66; Bigelow and Schroeder, 1936: 340; McKenzie, 1939: 16.

Lionurus (*Nezumia*) *bairdii* Gilbert and Hubbs, 1916: 146.

Coryphaenoides bairdii Schroeder, 1940: 235; Fowler, 1936: 1247.

General Characters. Head relatively small; about 15–16% of total length in complete specimens. Trunk rather short, distance from snout to anal fin about 25% of total length, 1.5–1.6 times length of head. Greatest depth about 80% of head, 12–15% of total length. Anus nearer to ventral than to anal fin, and surrounded by a naked area of club-shaped outline, the "shaft" of which extends forward between posterior portions of bases of ventrals. No separate naked area in thoracic region. Abdominal cavity extends rather far beyond origin of anal fin, for a distance equal to about 40% of length of head. About 24 simple, pyloric caeca.

Body Scales. Small, firmly adherent, squamation usually fairly complete in preserved specimens; about 40 scales in a longitudinal row from shoulder over a distance equal to that from snout to 1st dorsal fin. Each scale profusely covered with (70–90) very minute, subequal spines in a pattern of broadly V-shaped rows. On the back, forward of dorsal fin, a median row of spines becomes faintly differentiated from the rest on each scale by size and linear arrangement; in nuchal region of head other differentiated rows of spines are added to the median one, resulting in a slightly divergent arrangement of series of spines on each scale, which resemble the spines observed in *Chalinura*.

Head Scales. Entire head with fairly uniform cover of scales with minute spines generally arranged in diverging rows. No naked areas behind snout above; naked area below snout in well preserved specimens limited to a narrow median band in front. Squamation otherwise covers entire region below snout and suborbital ridge, the entire outer gill cover including exposed posterior portion of interoperculum and the entire ventral surfaces of rami of lower jaw. Branchiostegal rays and membranes and gular region without scales. Skin attached along lateral and circumorbital ridges, but not attached to dorsal

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[13] Also spelled *Macrourus* by some authors.

[14] Also spelled *bairdi* by others.

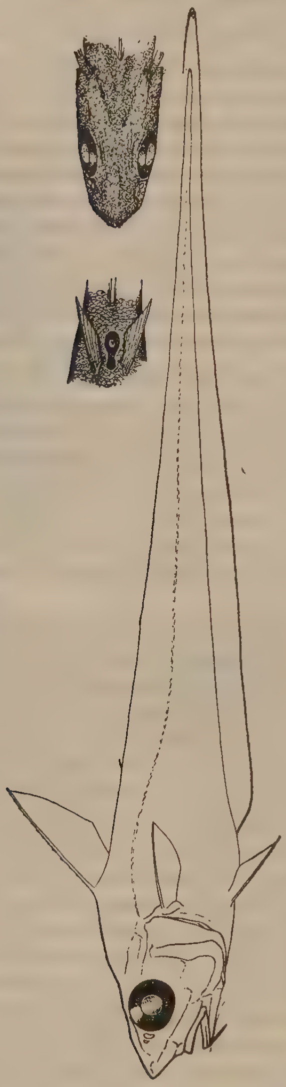

Figure 12.—*Nezumia bairdii* (Goode and Bean), with ventral view of anal area and dorsal view of head.

surface of head. Point of snout with spiny scales, but without clearly differentiated single terminal button. Ridges on head blunt and inconspicuous, obscured by small but thick and furry-looking scales.

Head Characters. Dorsal profile of head slightly concave above orbits, slightly convex before and behind. Snout prominent, bluntly pointed, rising from upper lip at a general angle to the horizontal of about 45°; snout in dorsal view converging at an angle of about 105°; length from orbits about 30%, median ventral length from mouth about 26%, of head. Mouth moderate, upper jaws about 30% of head. Premaxillaries extend to corner of lips. Barbel small and thin, 8–10% of head. Eyes rather large, lateral, subcircular or slightly elongate; diameter of orbit 33% of head; upper margins of orbits form wide, shallowly-indented curves in the lateral outlines of top of head. Interorbital width moderate, 1.2–1.3 in orbit, 25–27% of head. Posterior free margin of preopercle rises almost vertically at a general angle of about 85° to the horizontal, its lower corner not produced. Suboperculum broadly and fairly deeply emarginate between its upper and lower portions, exposing a small segment of upper branchiostegal rays and membrane. Interoperculum with wide posterior lamellae extending well beyond preoperculum, broadly adnate to the lower wing of suboperculum, which forms the rounded lower posterior corner of outer gill cover. First gill slit constricted, only about 15% of head, or less. 7 reduced gill rakers on lower limb of second arch, appearing as transverse ridges rather than free rods or tubercles.

Teeth. In both jaws in broad bands; those in lower jaw subequal, outer teeth in upper jaw slightly enlarged.

Fins. Pectorals conspicuously in advance of 1st dorsal fin, the ventrals between 1st dorsal and pectorals. 1st dorsal fin high, its highest spine about 80–100%, its base about 30%, of head; distance from snout to 1st dorsal fin 15–25% longer than length of head. Origin of 2nd dorsal far behind origin of anal fin, which is well behind the vertical from end of base of 1st dorsal. Distance from anterior end of ventral fin base to origin of anal rather short, 45–55% of head. Paired fins short; length of pectorals 55–60% of head. Longest ventral ray scarcely produced beyond the rest, 40–50% of head.

D_1. 12 V. 7 P. about 16

General coloration. Dark brown. Oral cavity, gill cavity and peritoneum black.

Size. Reaches about one foot.

Range. A species of wide range in the western Atlantic, occurring from the West Indies to the Gulf of St. Lawrence. Recorded only once from the vicinity of the Azores in the eastern Atlantic, but not as yet reported from the coastal waters of Europe. Ranges up to 50 fathoms depth, very abundant below the 100 fathom contour.

Nezumia hildebrandi, new species

Figure 13.

Macrourus holotrachys Hildebrand, in Longley and Hildebrand, 1941: 33.
Not *Macrurus holotrachys* Günther, 1878: 24; 1887: 136, pl. XXVIII, fig. B.

Five macrourids in the Longley collections from Tortugas were tentatively identified by Hildebrand as *Macrourus holotrachys* Günther. Through the courtesy of the U. S. National Museum the author has had opportunity to examine four of these specimens and has come to the conclusion that they represent a new species. That the specimens cannot belong to *M. holotrachys* is shown by the uniform cover of peculiarly flat and wide spinules on the scales, while Günther's illustration of the striated appearance of his species is fully borne out by the description, in which he stated: "Each *scale* with a median series of spinelets, and with two or more isolated spinelets besides; the median are the strongest, forming with their fellows continuous longitudinal lines on the body." In addition, there is also the advanced origin of the second dorsal fin in *M. holotrachys*, already commented upon by Hildebrand, and the fact that the lower surfaces of the head (below the suborbital ridge) are not naked in *N. hildebrandi*, as described for *M. holotrachys*.[15] *N. hildebrandi* is also clearly distinct from *N. bairdii* by the characters given in the key.

General Characters. Head rather small; 16–19% of total length in complete specimen. Trunk short; distance from snout to anal fin 1.5–1.6 times length of head, 27–28% of total length. Greatest depth of body about 80% of length of head. Anus immediately behind bases of ventrals, in the anterior portion of a broadly elliptical naked area which extends from the ventral fin bases approximately half-way to origin of anal fin. Abdominal cavity extends beyond origin of anal fin for a distance equal to about 27–30% of head. About 22 simple pyloric caeca.

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[15] The writer would like to add to the above comparison the comment that *M. holotrachys* is apparently not a *Nezumia*, but may possibly be an austral congener of the otherwise boreal genus *Macrourus* in the narrower sense in which this generic name is applied in the present report. All the features mentioned above—the ridge-like arrangement of spines on the scales, the advanced origin of the second dorsal fin (actually shown before the origin of the anal fin in Günther's figure) and the nakedness of the lower surface of the head—point toward *Macrourus*, sensu stricto. These indications gain further significance from the position of the anus (at origin of anal fin), which is suggested in Günther's figure of *M. holotrachys*, and which apparently is confirmed by the statement in the text that the distance from the vent to the isthmus is equal to the length of the head without snout. Apart from the apparent agreement in the position of the anus relative to the anal fin, the unusually great length of the abdomen, characteristic of the genotype *M. berglax* (see pp. 17, 50), evidently occurs also in *M. holotrachys*. If the relationship here guessed at should prove valid, it will provide another interesting example of "bipolar" distribution of closely related forms.

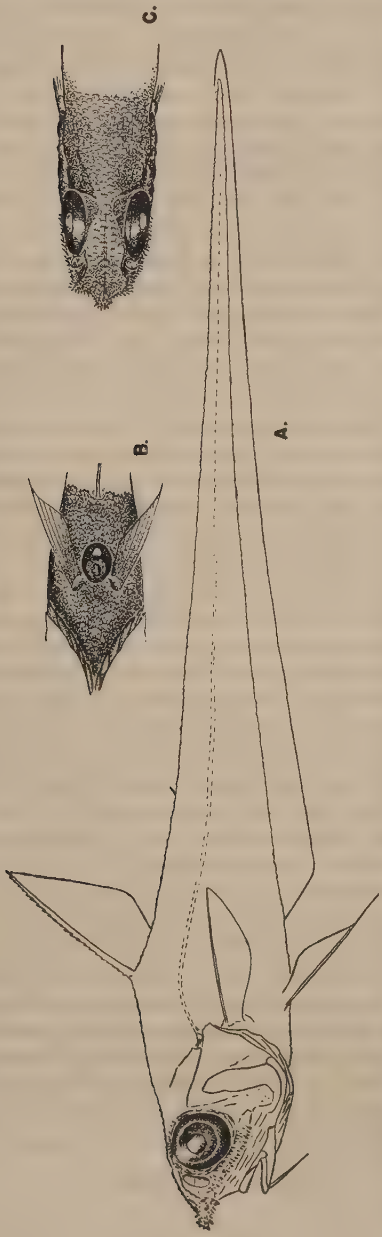

Figure 13.—(A) *Nezumia hildebrandi*, n. sp.; (B) ventral view showing the relative position of anus and naked area to ventral fins; (C) dorsal view of head.

Body Scales. Small, moderately adherent, about 36–38 scales in a longitudinal row from the shoulder over a distance equal to that from snout to 1st dorsal fin; each scale with about 20–40 broad, flattened, double-edged spinules with broadly arched points, resembling points of a short Roman gladiator sword; spinules arranged in quincunx, their width resulting in an imbricated pattern.

Head Scales. Entire head apparently with a fairly uniform squamation of ctenoid scales; no naked areas behind snout above; area below snout, in front of lateral ethmoids, with only some scattered scales, but predominantly naked; area between mouth and suborbital ridge behind lateral ethmoids with uniform, imbricated squamation; scales at tip of snout and along its anterior lateral edges with enlarged spinules; exposed portion of interoperculum with scales; branchiostegal membranes and gular region naked. Point of snout with a symmetrical pair of thickened, spinulose scales. Ridges on head probably not very conspicuous in normal state, but rather prominent in the alcohol-desiccated type specimen.

Head Characters. Snout prominent, pointed, rising from upper lip at a general angle to the horizontal of about 45°; straight lines from lateral ethmoids to point of snout converging at an angle of about 120°, but with rather deep emarginations in lateral outlines behind the point; length of snout from orbits about 26–30%, median ventral length from mouth about 24–26%, of head. Mouth moderate. Upper jaws about 30% of head. Premaxillaries extend to corner of lips. Barbel moderate, thin, about 15% of head. Eyes large, lateral, slightly oblique; horizontal diameter of orbit about 33–38% of head; upper margins of orbits forming shallow emarginations in the lateral outlines of top of head. Interorbital space relatively narrow, about 1.6–1.8 in orbit, or about 20% of head. Posterior free margin of preopercle rises at a slight angle forward of the vertical, its lower corner not produced. Posterior margin of suboperculum not emarginate. Upper branchiostegal not exposed. Posterior rounded corner of interoperculum broadly exposed beyond preoperculum, with scales on the exposed portion. First gill slit constricted, about 15% of head. 7 reduced gill rakers (spiny transverse ridges) on lower limb of second arch.

Teeth. Subequal, in broad bands in both jaws.

Fins. Pectorals conspicuously in advance of 1st dorsal fin, the ventrals between verticals of pectorals and 1st dorsal. Serrate spine of 1st dorsal about 80%, base of 1st dorsal about 25–28%, of head; distance from snout to 1st dorsal fin about 25% longer than head. Origin of 2nd dorsal fin far behind origin of anal fin, which is immediately behind the vertical from end of base of 1st dorsal. Paired fins moderate, pectorals and longest ventral ray apparently about equal, measuring 50–60% of length of head. Longest ventral ray apparently produced beyond the rest only slightly, but fins are in a poor condition. Distance from anterior end of ventral fin base to origin of anal quite short, only about 40–45% of length of head.

D. 11 V. 9 P. about 20

General Coloration. Apparently fairly light, with tip of first dorsal fin black. Oral cavity, gill cavity and peritoneum black.

Size. A small species reaching a size of about one foot.

Range. Known only off Havana, Cuba, in 154 fathoms. Type No. 47625 in the U. S. National Museum.

Genus **CETONURUS** (Günther, 1887)

Cetonurus (subgenus of *Macrurus*) Günther, 1887: 124, 143; Goode and Bean, 1895: 411.

Head large; its length about 20% of total length. Branchiostegal rays 7. Trunk very short; distance from snout to anal fin only about 30% longer than head. Anus approximately in center of a relatively wide oval or circular area of scaleless black skin, and separated from origin of anal fin by the radius of this area; nearer to anal fin than to bases of ventrals. Only about 10 simple pyloric caeca. Scales on body small, firmly adherent, strongly ctenoid with rather erect spines; upper row of scales along base of 2nd dorsal fin conspicuously enlarged. Small, button-like, spiny scute at point of snout. Squamation on head otherwise uniform without naked areas either above or below snout. Scales present in irregular double row in mid-ventral region of gular membrane, but absent from branchiostegal membranes. Exposed parts of interoperculum completely scaly. Snout high and moderately prominent. Skull with high ridges below skin, which are not conspicuous externally, but which give the head a soft, spongy character. Mouth rather small, very low; length of upper jaws only about 25% of length of head. Less than 15 gill rakers on lower limb of second arch. Eyes moderate, entirely lateral. Interorbital space very wide, more than 30% of length of head. Posterior and lower portions of interoperculum broadly exposed beyond preoperculum. Suboperculum not emarginate. Upper branchiostegal completely hidden. Teeth in bands in both jaws, with enlarged outer series in upper jaw. Dorsal spine serrate. Anterior rays of 2nd dorsal fin minute. Origin of anal fin about midway between bases of ventrals and end of abdominal cavity; distance from anterior end of ventral fin bases to anal fin about 20–30% of length of head. Fins small, particularly the ventrals, which have 9 rays.

Cetonurus globiceps (Vaillant, 1888)

Figures 14, 9 (p. 31).

Macrurus globiceps (Vaillant) Filhol, 1884: 185, fig. 2.
Hymenocephalus globiceps Vaillant, 1888: 386; Roule, 1919: 134.
Macrurus (*Cetonurus*) *globiceps* Murray and Hjort, 1912: 398; [*Macrurus* (*Cetonurus*) sp. Koefoed, 1927: 96, pl. V, fig. 9].
Cetonurus globiceps Fowler, 1936: 467, fig. 227.
Hymenocephalus crassiceps Vaillant (*nec.* Günther), 1888: 214, pl. XX, figs. 1–1e.

General Characters. Head bulky, deep and wide, its length about 20% of total length, or more. Distance from snout to origin of anal fin about 1.3 times length of head, or about 27% of total length. Tail tapering rapidly from trunk; depth of body about 40% of head, 16% of total length. Abdominal cavity extends beyond origin of anal fin for a distance equal to about 25% of length of head. 10 simple pyloric caeca, 14–15% of length of head.

Body Scales. Small, firmly adherent, about 60 in a longitudinal series from shoulder over a distance equal to that from snout to dorsal fin. A row of enlarged scales on each side along base of 2nd dorsal fin, the linear dimensions of these scales being approximately twice the corresponding linear dimensions of average scales below on body. Each scale with about 12–20 long, rather erect, spinules.

Head Scales. Squamation on head complete and uniform, without naked areas either above or below the snout. Point of snout with a spiny scute. Scales along nasal and suborbital ridges fixed, skin and squamation on head otherwise loosely connected with skeleton; scales cover entire ventral surfaces of the rami of lower jaw and are continuous with squamation of cheeks; an irregular double row of separate scales along middle of gular region below, but none on branchiostegal rays or membranes; exposed parts of interoperculum completely scaly. Head tumid, with high internal ridges which become conspicuous in shrunken specimens, but are hidden below the loosely connected skin in fresh and uninjured material.

Head Characters. Snout high, fairly prominent and rather pointed in lateral view, quite blunt in dorsal perspective; snout from orbit 36–37% of head; the line from upper lip to point of snout ascends at an angle of about 60° with the horizontal, its length about 30–32% of length of head; greater part of the depth of head is below level of axis of tail, resulting in a rather low dorsal profile of head; snout in dorsal view broad and blunt, the angle of convergence about 115°, the width between lateral ethmoidal corners slightly more than 25% of length of head, conspicuously wider than interorbital space. Mouth small, inferior. Upper jaws 25% of head. Barbel rudimentary, about 4% of head. Eyes moderate, subcircular, entirely lateral; horizontal diameter of orbit about 28% of head; upper margin not indented in the lateral outline of top of head, as viewed from above. Interorbital space wide, about 35% of head, 1.2–1.3 times orbit. Posterior free margin of preopercle rises at a general angle to the horizontal of about 75°, its lower corner very broadly rounded. Upper branchiostegal completely hidden. Upper portion of suboperculum not emarginate. Interoperculum with posterior corner and entire lower margin exposed beyond preoperculum. Posterior margin of outer gill cover entire, without free subopercular or interopercular projections. First gill slit restricted, its length only 10–12% of head. About 10 gill rakers on lower limb of second arch.

Teeth. In bands in both jaws.

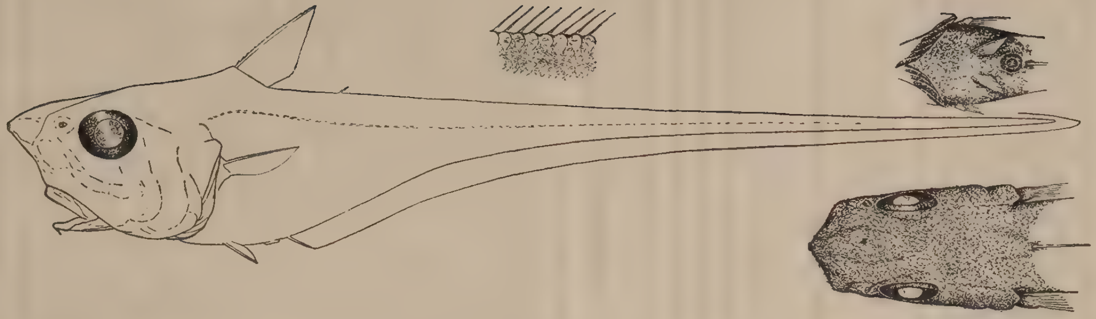

Figure 14.—*Cetonurus globiceps* (Vaillant), with view of enlarged scales from base of dorsal fin, as well as dorsal view of head and ventral view of anal area.

Fins. Very small. Origins of 1st dorsal, pectoral and ventral fins in approximately the same vertical. 1st dorsal base about 16%, its height about 45–50%, of head; snout to 1st dorsal fin less than 5% longer than head. Anterior rays of 2nd dorsal very small; origin of 2nd dorsal fin well behind origin of anal, which is much nearer to the vertical from the end of base of 1st dorsal. Distance from anterior end of ventral fin bases to origin of anal fin very short, only 23–25% of head. Length of pectorals about 30–35%, ventrals about 16%, of head.

D_1. 9 V. 9 P. 17

General Coloration. Dark. Oral and branchial cavities and peritoneum black.

Size. Does not exceed two feet in length.

Range. Although there is apparently no published record of this species from the western Atlantic, the collections of the U. S. National Museum were found to contain a specimen from "Albatross" station 2751, Nov. 28, 1887, 16° 54′ N., 63° 12′ W. Its distribution thus extends across the Atlantic in warm waters.

GRENURUS, new genus

Genotype *Grenurus grenadae,* new species.

Head short. Nape high and steep. Branchiostegal rays 7. Trunk short; distance from snout to anal fin less than 50% longer than head. Abdomen deep. Tail long and slender. No lense-shaped luminous organs. Anus surrounded by scaleless area, the posterior border of which is at origin of anal fin, which places vent well in advance of anal fin. Only about 8 simple pyloric caeca. Scales ctenoid, with a moderate number of subequal spinules arranged in parallel rows. Point of snout with well defined terminal scute. No modified or enlarged scales along back. Interoperculum with scales on its exposed portion. Snout blunt, moderately prominent. Mouth moderate. First gill slit restricted. Less than 15 gill rakers on lower limb of second arch. Eyes large, lateral. Suborbital ridge fairly strong, but not rigidly connected to preoperculum. Teeth in bands in both jaws. Dorsal spine probably serrate (see p. 49). Base of 1st dorsal descending steeply from its elevated anterior end. Origin of anal fin approximately midway between ventral fins and end of abdominal cavity. Distance from ventrals to anal fin less than half of greatest depth of body.

It seems unfortunate to have to introduce a new genus at this point, but the procedure seems more practical than any attempt to broaden the definition of some other genus to enable it to accommodate also the new species described in the following. The basis upon which the genus is established will be apparent from the manner in which it is differentiated from related genera in the key on page 21. The position of the scaleless periproct, the low number of pyloric caeca, and the advanced origin of anal fin are the most important features distinguishing *Grenurus* both from *Ventrifossa* and from *Nezumia.* The genotype of *Grenurus* is also apparently the smallest macrourid species known from the western Atlantic. The type specimen is a fully mature female, with large eggs, ready to spawn at a length which cannot have exceeded 10 inches previous to the loss of the tip of the tail.

Only the genotype known.

Grenurus grenadae, new species[16]

Figures 15, 9 (p. 31).

General Characters. Head and trunk relatively short, tail very long and rapidly constricted from body. Head only about 15% of total length in a specimen which is not entirely complete as to tail. Distance from snout to anal fin less than 22% of total length, about 40% longer than head. Greatest depth slightly greater than length of head. Abdominal cavity extends backwards above anal fin for a distance of about 40–45% of length of head. Anus in a subcircular, scaleless area of black skin, which separates it from origin of anal fin by a quite conspicuous distance, although it remains distinctly closer to anal fin than to ventrals; no separate scaleless area anterior to the periproct. 8 simple pyloric caeca.

Body Scales. Adherent, moderate in relation to total size; about 35 scales in a longitudinal series from shoulder over a distance equal to that from snout to 1st dorsal fin; each scale with about 20–40 small, depressed spinules arranged in 5–7 subparallel, linear series.

Head Scales. Although the ridges on the head are only moderately prominent, they become conspicuous by the distinct differentiation and increased spinous armanent of their scales. Point of snout with a circular, button-like scute with radiating spinules. Edge of snout between its point and tips of lateral ethmoids not reinforced with modified scales. Lateral ethmoids and suborbital ridges to below last third of orbit strongly reinforced by thickened, spinous scales. Posterior part of suborbital ridge weaker and its connection with preoperculum not rigid. Although many scales are missing on the type specimen, it appears that there are no naked areas above snout. Region below snout and suborbital ridge scaleless almost to end of upper jaws. Entire gill cover scaly. Interoperculum with a few scales (2–6) at its posterior corner and along its lower margin. It is unclear whether or not scales have been present on the branchiostegal membrane, but there is some suggestion that a few scales may have occurred on the basal portions of some of the lower branchiostegal rays.

[16] The U. S. National Museum collection contains a specimen labeled "Lionurus grenadae Type" without indication of authorship. There is no published description of such a species, nor has it been possible to discover the author of the label. The specific name is retained in courtesy to the anonymous ichthyologist who first realized that he had a new species before him.

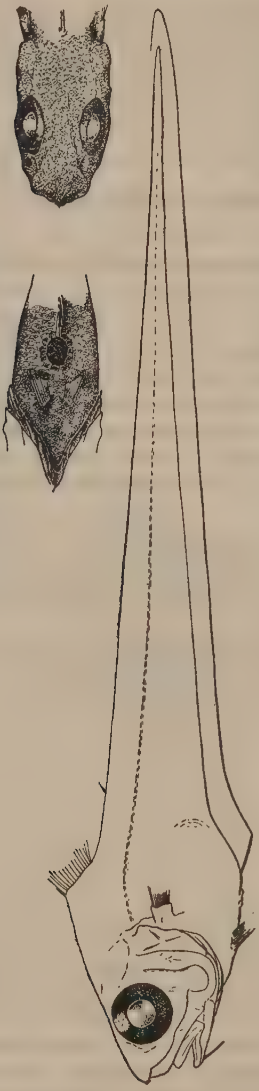

Figure 15.—*Grenurus grenadae* (Anon.), n. sp., with ventral view of anal region and dorsal view of head.

Head Characters. Nape and back rise steeply to the elevated anterior end of the steeply inclined base of 1st dorsal. Dorsal profile of head and nape confluent, rising from the horizontal at a general angle of about 20°. Snout slightly prominent, blunt, rising from the upper lip at a general angle to the horizontal of about 75°; in dorsal view rather truncated (Fig. 15); length from orbits about 30%, height from mouth about 20%, of length of head. Mouth moderate. Upper jaws about 35% of head. Premaxillaries reach nearly to corner of mouth. Barbel thin but relatively long, 20–25% of length of head. Eyes relatively large, lateral, subcircular; diameter of orbit 37–40% of head; upper margins of orbits slightly concave in dorsal view. Interorbital width moderate, 1.7 in orbit, about 22–23% of head. Posterior free margin of preopercle rises almost vertically, with lower corner broadly rounded. Suboperculum only slightly emarginate. Branchiostegal rays completely hidden when withdrawn. A small posterior corner and narrow inferior margin of interoperculum throughout its length exposed beyond preoperculum. Relationship between suboperculum and interoperculum essentially as in *V. bairdii.* First gill slit constricted, about 18% of length of head. 9 reduced gill rakers on lower limb of second arch.

Teeth. In bands in both jaws, with somewhat enlarged outer teeth in upper jaw.

Fins. Dorsal fin has its origin well behind bases of pectorals; dorsal fin is on an almost straight line through pectorals to bases of ventrals, which are anterior to other fins. 1st dorsal fin base length about 25% of length of head; snout to 1st dorsal fin about 30% longer than head. Origin of 2nd dorsal well behind end of base of 1st dorsal. Distance from anterior end of ventral fin base to origin of anal fin quite short, only 40–45% of the length of head. Origin of anal fin approximately below end of base of 1st dorsal. Since the longer fin rays of all fins are broken and incomplete, it is impossible to make definite statements about the sizes of the fins, except that there is no suggestion of unusual dimensions in the parts shown. The second dorsal spine is broken too close to the base to prove conclusively whether or not the spine has been serrate, but the leading edge of the stub is trenchant, and its general appearance agrees with the proximal portion of the serrate rather than the smooth type of spine.

D_1. 12 V. 11–12 P. 20

General Coloration. Black. Oral cavity, gill cavity and peritoneum also black.

Size. In spite of its small size of only 199 mm. in total length (very nearly complete, although a few of the ultimate caudal vertebrae are missing), the type specimen (U. S. Nat. Mus., No. 47625) is a fully mature female with large, apparently quite ripe eggs.

Range. Only the type specimen known; from "Blake" Station 299, in 576 fathoms, off Grenada.

Genus **MACROURUS** Bloch, 1787

Macrourus Bloch, 1787a: 78; 1787b: 122.

Head fairly large, its length 20% of total length, or more. Branchiostegal rays 6. Trunk very long; distance from snout to anal fin about 40% of total length, about 70% longer than head. Anus at origin of anal fin. No scaleless areas on body. About 19 pyloric caeca. Scales on body large, each with a serrate median keel formed by a series of strong spines closely applied to each other. Ridges on head strongly developed, with conspicuously modified scute-like scales. Ventral surface of snout scaleless; three enlarged scales in symmetrical arrangement at tip of snout. Snout prominent, pointed. Mouth moderate to large; upper jaws more than ⅓ length of head. Gill rakers reduced, less than 15 on lower limb of second arch. Eyes large, about ⅓ of head. Preopercular margin oblique. Suboperculum not emarginate. Interoperculum completely hidden behind preoperculum. Upper branchiostegal ray not exposed. Teeth in irregular double row in lower jaw, a band in upper jaw. Dorsal spine serrate. Anterior rays of 2nd dorsal fin well developed and placed well in advance of anal fin. Origin of anal fin in last fourth of distance from ventrals to end of abdominal cavity, the distance from ventrals to anal being more than ⅔ of length of head. Ventral fins with 8 rays.

Macrourus berglax Lacépède, 1802

Figures 16, 9 (p. 31).

Macrourus berglax[17] Lacépède, 1801: 170, pl. 10, fig. 1; Jordan, 1887: 919 [131]; Goode and Bean, 1895: 391, fig. 334; Jordan and Evermann, 1898: 2582; Bigelow and Welsh, 1925: 470, fig. 236; Jordan, Evermann and Clark, 1930: 205; Vladykov and McKenzie, 1935: 66, fig. LII.

Macrurus[18] *fabricii* Sundevall, 1842: 6; Collett, 1875: 128; 1885: 95; Goode and Bean, 1880: 7; Jordan and Gilbert, 1882: 811; Günther, 1887: 130; Lilljeborg, 1891: 242; Lütken, 1898: 23; Ehrenbaum, 1902: 116; Jensen, 1904: 271.

Coryphaena rupestris (nec. *Gunnerus*) Fabricius, 1780: 154.

Macrourus[17] *rupestris* (nec. *Gunnerus*) Bloch, 1787a: 80, pl. 177; 1787b: 123, pl. 177; Reinhardt, 1838: 116; Nilsson, 1855: 604; Günther, 1862, 390; Esmark, 1869: 527; Lütken, 1872–73: 4.

General Characters. Head fairly large, about 20–23% of total length, trapezoid to hexagonal in cross section. Trunk relatively very long, rounded; distance from snout to anal fin about 40% of total length, 1.7 times length of head. Tail compressed. Greatest depth about 70% of head. Abdominal cavity extends beyond origin of anal fin for a distance equal to about 16–17% of length of head. 19 long, simple pyloric caeca.

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[17] Also spelled *Macrurus*.

[18] Also spelled *Macrourus*.

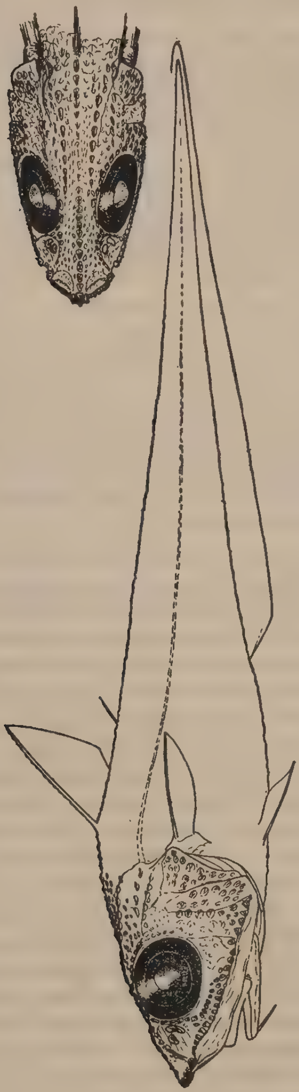

Figure 16.—*Macrourus berglax* Lacépède, with dorsal view of head.

Body Scales. Firmly adherent; scales uniform on all parts of body, without reduction of their size or armature in ventral region; about 36 scales in a longitudinal series from shoulder over a distance equal to that from snout to dorsal fin. Each scale on trunk and tail with a high median serrate ridge formed by a number of short strong spines closely applied to each other, some with additional faint diverging ridges.

Head Scales. Squamation on head differentiated by conspicuous rows of enlarged scales following the crests and ridges, with areas of smaller scales between; scales on head not imbricated, commonly not even in contact, but more or less separated, in the skin; scales along ridges on sides of head usually armed with several diverging serrate crests or rows of spines, while the smaller scales, especially on dorsal surfaces of head, carry a single crest only; scales along all ridges firmly fixed to skeletal parts, as are also larger scales on gill covers. Tip of snout with one median and one smaller, lateral, spiny scale on each side which gives the snout a bluntly three-pronged appearance in dorsal view. Suborbital ridge forms an externally continuous row of scales from tip of snout to lower posterior corner of outer lamellae of preoperculum, but without rigid internal connection from suborbital bones to preoperculum; entire lower surface of head naked, except for a few scattered scales near suborbital ridge.

Head Characters. Entire appearance of head shows strong resemblance with the genus *Coelorhynchus* in regard to general form, suborbital ridge and heterogeneous squamation. Dorsal profile of head inscribed in a gently convex curve from nape to snout. Snout prominent, rising from upper lip at a general angle to the horizontal of about 40°; cross-section of head trapezoid-ovate, with a prominent suborbital ridge sharply dividing the ventral from dorso-lateral surfaces; snout in dorsal view fairly blunt, forming an angle of about 110°; length from orbit about 32%, median ventral length from mouth about 21%, of head. Mouth fairly large, upper jaws 36% of head. While dentition of upper jaw extends to corner of mouth, the ossified premaxillary is apparently considerably shorter, although this may be due to decalcification in the available specimen. Barbel moderate, about 10–12% of head. Eyes very large, oval; vertical diameter about 1.2 in horizontal diameter, which equals about 33% of length of head. Interorbital width 1.9–2.0 in horizontal diameter of eye, about 17% of head. Sides of head converge towards top at a general angle of about 40° (each side about 20° to the vertical), causing the entire rims of orbits to be exposed in dorsal view, with the upper rims thus forming wide emarginations in the lateral outlines of top of head. Preopercle's posterior free margin rises at a general angle of about 75–80° to the horizontal. Suboperculum long, narrow, not emarginate. Upper branchiostegal completely hidden. Lower corner of outer gill cover formed by suboperculum alone. Interoperculum is completely hidden behind preoperculum, and does not make contact with suboperculum. First gill slit reduced to about 10% of head. Lower limb of second arch with 6–11 wart-like, reduced gill rakers.

Teeth. In an irregular double row in lower jaw, in a band in premaxillary. All small, none enlarged.

Fins. Relatively small, with exception of 2nd dorsal fin, which is fully developed with rays of normal size extending to its anterior end. Snout to 1st dorsal about 15% longer than head; base of 1st dorsal about 25–26%, its height about 50%, of head. Origin of 2nd dorsal well in advance of origin of anal fin; second ray of 2nd dorsal fin about 10% of head. Pectorals slightly, but distinctly, in advance of 1st dorsal. Length of pectorals about 40% of head. Ventrals directly below, or very slightly in advance of, pectorals; length of outer ventral ray, which is only slightly produced, about 35% of head. Distance from anterior end of ventral fin base to anal fin very long, 70–75% of head.

D. 10 V. 8 P. 18

General Coloration. Internal surfaces dark, external color unknown.

Size. More than three feet.

Range. An Arctic species occurring on both sides of the North Atlantic, from northern Norway northward in the east, and southward to New York in the west. Previously common in the Gulf of Maine, but now rare (*vide* Bigelow and Welsh, 1925). Caught from 100 to over 1500 fathoms depth.

Genus **NEMATONURUS** (Günther, 1887)

Nematonurus (subgenus of *Macrurus*) Günther, 1887: 150.

Branchiostegal rays 6. Trunk long, distance from snout to anal fin nearly twice length of head, which is approximately same as depth of body. Tail moderate, 60–70% of total length. Anus at origin of anal fin, without surrounding or preceding scaleless areas. About 10–12 pyloric caeca. Scales moderate or small, ctenoid, with spines arranged in extremely regular, well separated, subparallel series giving to each scale a striated appearance. Scales on head imbricated except in region below snout, where they are scattered or absent. No specially modified button-like scute at point of snout. Ventral surface of snout generally scaleless. Snout low but prominent. Mouth moderate or small, inferior. Less than 15 gill rakers on lower limb of second arch. Eyes small. Posterior margin of preoperculum subvertical. Interoperculum extends well beyond corner of preoperculum. Upper branchiostegal completely hidden behind opercular bones. Teeth in upper jaw in 2 distinct and well separated series; single series in lower jaw. 1st dorsal fin with a long serrate spine. Origin of 2nd dorsal well behind origin of anal fin, its anterior rays rudimentary. Origin of anal fin in last fourth of distance from ventrals to end of abdominal cavity; distance from ventrals to anal fin more than ⅔ length of head. Ventrals with 10 rays; outer ray produced.

Nematonurus armatus (Hector, 1875)

Figures 17, 9 (p. 31).

Macrurus armatus Hector, 1875: 81.

Macrurus (*Nematonurus*) *armatus* Günther, 1887: 150, pl. XL, fig. A; Koefoed, 1927: 109.

Nematonurus armatus Schroeder, 1940: 233.

Coryphaenoides gigas Vaillant, 1888: 232, pl. XX, figs. 2–2c.

Nematonurus gigas Roule, 1916: 21; 1919: 87, pl. III, figs. 1, 1a.

Macrurus asper Goode and Bean, 1883: 196.

Macrurus goodii Günther, 1887: 136 (substitution for *Macrurus asper* Goode and Bean, preoccupied).

Nematonurus goodii Jordan, Evermann and Clark, 1930: 203.

Hymenocephalus[19] *goodei* Goode and Bean, 1895: 407, fig. 340.

Macrurus (*Hymenocephalus*) *goodei* Lütken, 1898: 26.

Nematonurus goodei Jordan and Evermann, 1898: 2571; Linton, 1901b: 479; Wilson, 1915: 688; 1920: 571.

Macrurus (*Nematonurus*) *goodei* Ehrenbaum, 1902: 117.

Coryphaenoides affinis Günther, 1878: 27.

Macrurus (*Nematonurus*) *affinis* Günther, 1887: 151, pl. XL, fig. B.

Koefoed (1927: 110) gives a valuable table of measurements of a number of specimens from the eastern Atlantic, identified by him as (*Nematonurus*) *armatus* Hector. In the accompanying table the range of variations recorded by Koefoed is compared with the ranges observed by the writer in western Atlantic material.

From this table it is evident that the distinction between *N. armatus* and *N. goodei* rests entirely upon the presence or absence of an inner row of teeth in the upper jaw. This feature, however, is one to which the writer would give only very slight significance, or none at all, in view of the character of the inner teeth. Although they are often of moderate size and readily observed, these teeth are also frequently very small and very easy to overlook, as the writer has had opportunity to ascertain from his own experience and from that of his colleagues. In addition to the variation in the size of the individual teeth, there are also wide variations in their number and in the length of the series. Under these circumstances specific distinctions seem quite unwarranted. *Nematonurus goodei* has therefore been synonymized with *N. armatus*.

The inadequate first description of *Macrurus asper* (Goode and Bean, 1883) apparently created a misleading impression of its appearance and affinities in the mind of Günther (1887: 136) when he renamed it *N. goodii*, since there

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[19] Apparently a *lapsus calami*, since Goode and Bean themselves explicitly state (p. 408) that "This species [*goodei*] belongs in the subgenus *Nematonurus* of Günther," a subgenus which these authors on subsequent pages of the same publication (p. 416) elevate to generic rank.

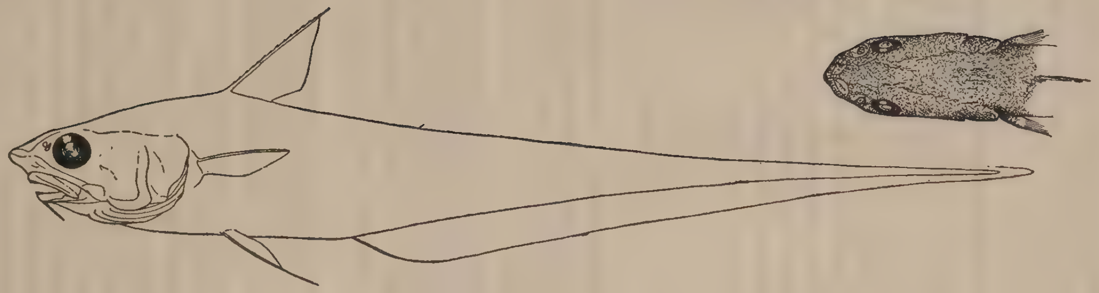

Figure 17.—*Nematonurus armatus* (Hector), with dorsal view of head.

does not seem to be much reason to doubt that his own *N. affinis* is also only a new name for the same form, placed in its proper position relative to other species (Günther, 1887: 151).

RANGES OF VARIATIONS IN SAMPLES OF *Nematonurus* FROM THE ATLANTIC

Inner series of teeth in premax.	absent	present	present
Designation	*"armatus"*	*"goodei"*	*"affinis"*
Total lengths in cm.	34–74*	26–45	25–33
Proportions in % of length of head:			
Snout to eye	25–31	24–30	25†
Orbit	17–23	19–22	25†
Interorbital	22–29	23–26	25†
Snout to first dorsal	118–132	121–123	—
Snout to anus	179–200	166–190	—
Base of first dorsal	25–36	27–29	—
Length of pectorals	58–60	50–68	—
Length of ventrals	52–74	52–68	—
Depth of body	75–105	75–80	—

* Koefoed's records, plus measurements of one specimen previously described by Schroeder (1940: 233) from the western Atlantic and re-examined by the writer.

† These three measurements are described as equal to each other and to one-fourth of the length of head.

General Characters. Head moderate; length about 17–19% of total length of complete specimen. Trunk long; distance from snout to anal fin about twice length of head, or about 35–36% of total length. Greatest depth about 1.5 in head, 12–13% of total length. Abdominal cavity extends beyond origin of anal fin for a distance equal to about 10–15% of length of head. 11 fairly thick, simple pyloric caeca.

Body Scales. Adherent, small; squamation uniform on all parts of body, without naked areas; about 38–40 scales in a longitudinal series from shoulder over a distance equal to that from snout to dorsal fin. Each scale with 20–30 small spines arranged in a number of divergent, very regular rows, of which the middle row is generally somewhat enlarged.

Head Scales. Squamation of head uniform, without conspicuously modified scales in any region. A pair of naked areas behind snout above, similar to those in *Chalinura;* the species also resembles *Chalinura* in the structure of individual scales. Area below snout and below entire suborbital ridge scaleless, except for some scattered scales posteriorly; this scalelessness below makes the suborbital ridge rather conspicuous, although not actually very prominent. Rami of lower jaw scaly below, at least throughout posterior half of their length. No scales in gular and branchiostegal regions, or on exposed part of interoperculum. Head externally very smooth without conspicuous ridges.

Head Characters. Snout rather small and low, but prominent; length from orbits about 27%, median ventral length of snout from mouth about 14%, of head. Postorbital part of head relatively very long; inclination of lower profile of snout about 45°; in dorsal view broadly angular, the angle of convergence about 105°. Mouth moderate. Length of upper jaw about 33% of head. Premaxillaries extend to corner of mouth. Barbel moderate, about 20% of head. Eyes small, lateral, circular; diameter of orbits about 20% of head, 1.2–1.3 in width of interorbital space, which is about 25% of head. Upper rim of orbit barely showing concave curvature in dorsal view. Preopercle's posterior free margin vertical, with a slight backward curvature toward the rounded lower corner. Upper branchiostegal ray completely hidden. Interoperculum with a long lamellar posterior portion extending beyond preoperculum to join with suboperculum in forming the lower posterior margin of outer gill cover. First gill slit about 1.5 in diameter of orbit. 10 reduced gill rakers on lower limb of second arch.

Teeth. In lower jaw moderate, arranged in a single series. Premaxillary dentition in two series, well separated from each other by a toothless ribbon between them. Teeth in outer series enlarged.

Fins. Origin of 1st dorsal and ventral fins well behind insertion of pectorals, the ventrals slightly in advance of 1st dorsal; snout to 1st dorsal fin 20–25% longer than head. Fins moderate. Base of 1st dorsal about 26, its height (length of serrate spine) about 75%, of head. Origin of 2nd dorsal fin far behind origin of anal, which is far behind end of base of 1st dorsal; anterior rays of 2nd dorsal fin very small. Length of pectorals about 50–55%, length of produced ventral ray about 55–60%, of head. Distance from anterior end of ventral fin bases to origin of anal fin very long, about 76% of length of head.

D_1. 10 V. 10 P. about 18–20

General Coloration. Dark brown. Mouth, gill cavity and peritoneum black.

Size. May attain a length of over three feet.

Range. Both sides of the North Atlantic in warm waters.

CARIBURUS, new genus

Genotype *Macrurus zaniophorus* Vaillant, 1888: 245.

Head moderate, its length about 18–22% of total length. Branchiostegal rays 6. Trunk moderate; distance from snout to anal fin 28–33% of total length, less than 70% longer than head. No naked areas in thoracic or abdominal region. Anus at origin of anal fin, without surrounding scaleless area. 8–15 pyloric caeca. Scales on body moderate or large, ctenoid, adherent. Spinules on scales in irregular quincunx, not in horizontal series. Point of snout with button-like, sculptured scute. Lower surface of snout completely scaly. Snout short and blunt. Ridges on head inconspicuous, or moderately developed without modified scales. Mouth moderate, upper jaws about ⅓ of length of head. Less than 15 gill rakers on lower limb of second arch. Eyes large, their diameter about ¼ of length of head, or more. Posterior part of interoperculum exposed beyond preoperculum. Suboperculum not emarginate. Upper branchial ray not exposed. Teeth in bands in both jaws. Dorsal spine serrate. Anterior rays of 2nd dorsal fin rudimentary, beginning far behind origin of anal fin. Origin of anal fin in last third of distance from ventrals to end of abdominal cavity, the distance from ventrals to anal fin being about 40–60% of length of head. Ventral fins with about 10 rays.

It is not without hesitation that the two species, *C. zaniophorus* and *C. mexicanus*, are referred to the same genus. Neither of these two forms can be well fitted into any of the other western Atlantic genera dealt with herein without producing an undesirable broadening of generic definitions, which would be contrary to one of the purposes of this investigation. On the other hand, we also find such dissimilarities between the two species that there is considerable temptation to separate them generically from each other, as well as from the remaining macrourids. By so doing one would be able to sharpen the definition of the genus *Cariburus*, particularly with regard to the following features shown by the genotype, but not shown by *C. mexicanus:* the very long intestine (9–10 times the length of the abdominal cavity); the perpendicular free margin of the preopercle; the *thick* and *scaly*, broadly exposed, interoperculum; the strikingly thickened barbel.

If *C. mexicanus* is segregated, the characters just mentioned should be added to the generic diagnosis of *Cariburus*. In *C. mexicanus* the intestine is of normal length (less than 5 times length of abdominal cavity), the margin of the preopercle is quite oblique; the interoperculum is not thickened and is without scales, although pigmented like the surrounding exposed skin, and the barbel is thin as in other macrourids.

KEY TO THE SPECIES OF *Cariburus*

1a. Barbel very thick, fleshy. Interoperculum thick, broadly exposed beyond preoperculum, the exposed portion with scales. Preopercular margin vertical. *zaniophorus* (Vaillant), below

1b. Barbel thin, filamentous. Interoperculum thin, projecting conspicuously beyond preoperculum, but without scales on the exposed portion. Preopercular margin inclined..*mexicanus*, n. sp., p. 62

Cariburus zaniophorus (Vaillant, 1888)

Figures 18, 9 (p. 31).

Macrurus zaniophorus Vaillant, 1888: 245, pl. XXII, figs. 4–4a; Koefoed, 1927: 86, fig. 22.

The specimen obtained by the "Atlantis" in the Gulf of Mexico agrees minutely with the descriptions and measurements of eastern Atlantic examples as given by Vaillant and by Koefoed, except in regard to the size of the eyes. In four specimens examined by Koefoed, the diameter of the eyes equaled 34.6–36.5 per cent of the length of head. In the specimen from the Gulf of Mexico the diameter of the orbit is slightly less than 30 per cent of head. The writer would have been inclined to give this difference greater weight if it were not also for the fact that the Gulf specimen is patently to be considered a much larger one than any of those described by Koefoed. In the largest of the latter the head measured only 55 mm., in our specimen its length is measured as 77 mm., or 40 per cent more. This larger "real" size is obscured by a truncated tail and regenerated caudal fin, but is probably enough to account for the difference in the relative sizes of the eyes.

General Characters. Since the available specimen has obviously lost its tail and formed a secondary false caudal fin, it is not possible to speak with exactitude about the normal proportions of the entire fish. But on the basis of general appearance, it seems indicated that head and trunk would normally be in moderate proportion to total length, somewhat as in *Coelorhynchus.* Certainly a very large head and trunk, as in *Oxygadus occa*, seems excluded, and an extremely long tail (as in *Coryphaenoides*), reducing the relative proportions of the anterior parts, seems equally unlikely. Distance from snout to anal fin about 1.5–1.6 times length of head. Greatest depth of body about 80% of head. 14 simple pyloric caeca. Abdominal cavity extends beyond origin of anal fin for a distance equal to 18–20% of head. Intestine very long, about 8–10 times length of abdominal cavity, forming a double backward and a double forward loop.

Body Scales. Uniform on all parts, without naked fossa below or further modifications in other regions. About 43–45 scales in a longitudinal series from shoulder over a distance equal to that from snout to 1st dorsal fin. Each scale with numerous (120–160) fairly short, but quite strong, spinules arranged in V-shaped series.

Head Scales. On all surfaces of head fairly uniform morphologically, varying mainly as to size and arrangement; those in median dorsal region of head and neck not uniformly graduated as to size; scales in anterior, occipital region of nape smaller than both those behind on neck and those forward on frontal region of the skull. Scales on dorsal surface of the snout generally not smaller than those of interorbital region; they become smaller only toward the extreme forward end, on the sides and on the ventral surface. Median row of scales above snout, extending to anterior portion of interorbital space, well differentiated from the general squamation by their arrangement into a linear, but not raised, series of scales with square exposed surfaces. Close examination also reveals linear rows along anterior part of suborbital ridge below nasal region, and also above nostrils, but these are not conspicuous in general appearance. Point of snout with a small button-like shield, with faint radiating ridges. Entire lower surface of snout scaly, including median line in front. No naked

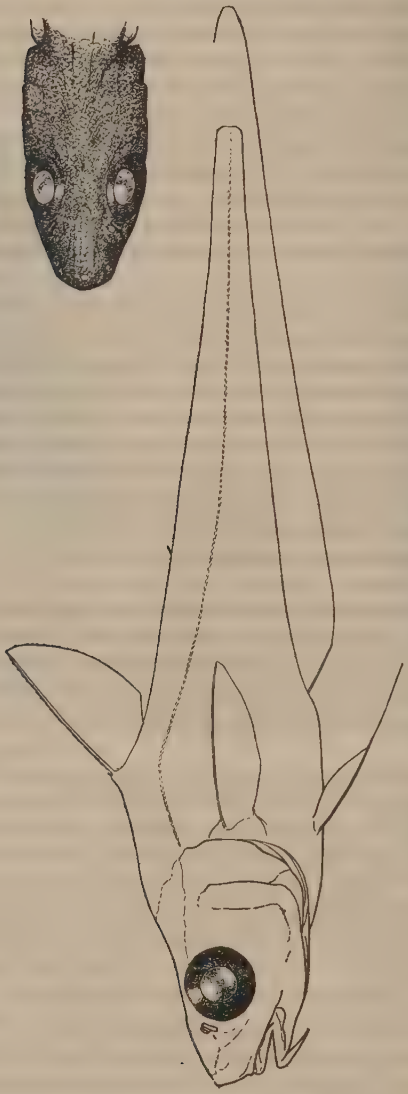

Figure 18.—*Cariburus zaniophorus* (Vaillant), with dorsal view of head.

areas above snout. Scales on cheeks rather large, the posterior scales on gill cover not smaller than anterior scales on body between pectoral fin and lateral line. A wide (high) area of greatly reduced scales in post-temporal region, creating a sharp, highly arched line of demarkation from the large scales on side of neck. Scales absent in gular and branchiostegal regions. Head without externally conspicuous ridges. Skin on head firmly attached to outer edges or surfaces of bones on sides of head, as well as around orbits and in median of snout above; also, the skin is very closely applied, although not actually rigidly fixed, to the exposed dorsal surfaces of skull itself in interorbital region and behind.

Head Characters. Snout broadly rounded in dorsal view, blunt in lateral perspective, rising at an angle of about 75° with the horizontal; dorsal profile concave above orbits, slightly convex over snout, and strongly convex over occipital region; length about 28% of head; height of snout (ventral length) from upper lip about 13%. Mouth moderate. Upper jaws about 31–32% of head. Premaxillaries extend to corner of mouth (corner of fleshy lips). Barbel short and very thick, its length only about 19% of length of head. its width at base nearly ⅓ of its length. Eyes large, circular; diameter of orbit about 29–30% of head. Interorbital space narrow, 1.7 in orbit, about 17% of head. Upper margins of orbits deeply indented in the lateral outlines of top of head as viewed from above. Preopercle's posterior free margin straight and perpendicular. Suboperculum not emarginate. Interoperculum projects considerably beyond preoperculum to margin of suboperculum, which it overlaps, its thick, exposed portion covered with normal scales. Dermal edge of outer opercular cover entire and continuous from operculum to interoperculum. About 12–13 tubercular gill rakers on lower limb of second arch. First gill slit almost obliterated, only about 5% of length of head.

Teeth. In jaws minute, in broad bands above and below, none enlarged.

Fins. Fairly large. Base of 1st dorsal about 28% of head, its height about 70%; origin of 1st dorsal fin far behind pectoral base; snout to 1st dorsal about 25% longer than head. First ray of 2nd dorsal far behind origin of anal fin. Anterior rays of 2nd dorsal almost rudimentary. Origin of anal fin only slightly behind end of base of 1st dorsal. Ventral fins directly below, or very slightly in advance of, pectoral fin base. Distance from anterior end of ventral fin bases to anal fin long, slightly more than half the length of head. Length of pectorals about 65–70% of head, length of produced ventral ray about 75%.

D_1. 11 V. 10 P. 22

General Coloration. Dark brown or brownish black on all parts, including lower surface of head (lower jaws, branchiostegal membranes, integuments between rami of lower jaw, and proximal ⅔ of barbel). Oral cavity and opercular cavity black; peritoneum dark.

Size. Probably does not exceed 18 inches in length.

Range. Eastern North Atlantic. Gulf of Mexico. One specimen from "Atlantis" St. 2823.

Cariburus mexicanus, new species

Figures 19, 9 (p. 31).

Type specimen, B.O.C. No. 2211; "Atlantis" Station 2853 Q, in the Gulf of Mexico.

General Characters. Head and trunk moderate, distance from snout to anal fin about 33% of total length, or 1.5–1.6 times the length of head, which is about 21–22% of total length. Greatest depth about 70–90% of head. Abdominal cavity extends backward beyond origin of anal fin for a short distance equal to about 17–18% of head. Intestine with a double backward, and single forward, loop, only 4–5 times as long as abdominal cavity. 9–10 simple, pyloric caeca.

Body Scales. Uniform, without naked fossa below, or modifications in other regions. About 45 scales in a longitudinal series from shoulder over a distance equal to that from snout to 1st dorsal fin. Each scale with a moderate number (10–15) of large strong spines in an irregular quincunx arrangement.

Head Scales. Scales on all surfaces of head normal; those in median region along dorsal surface of head and neck uniformly graduated in size from smaller scales anterior to orbits to somewhat larger scales before dorsal fin. Median row of scales above snout not distinctly set off from others, even under close examination. Point of snout with a bony shield or button with bold radiating sculpture. Posterior scales on upper part of gill cover conspicuously smaller than anterior scales on body above pectoral fin. Entire lower surface of snout scaly, including median region in front; upper surface without naked areas. Gular and branchiostegal regions without scales. Scales in post-temporal region only moderately reduced in a narrow band above upper edge of operculum. Skin on head firmly attached to outer edges or surfaces of bones on sides of head, as well as around orbits and in median of snout above (anterior to orbits); but skin is not fixed directly to the bones of skull itself in interorbital region, or on its dorsal surface behind orbits (parietal and supraoccipital regions). Head without any externally visible ridges above, but a well marked suborbital ridge extends from nasal region to beyond eye without quite reaching to lower posterior corner of *anterior* outer edge of preoperculum.

Head Characters. Dorsal profile of head slightly concave above eyes. Snout moderately prominent, rather blunt, rising from mouth at a general angle with the horizontal of about 60°; broad in dorsal view, the general angle of convergence about 115°; length from orbits about 30% of head, median ventral length (height) from mouth 17–21%. Mouth moderate. Upper jaws about 31–34% of head. Premaxillaries extend fully to corners of fleshy lips. Barbel minute and thin, 9–10% of head. Eyes moderate, subcircular; diameter of orbit 25–28% of head. Interorbital space wide, 1.1–1.3 in diameter of orbit, 20–25% of head. Eyes moderately prominent in dorsal view, the upper margins of orbits forming shallow emarginations in the lateral outlines of top of head, as viewed from above. Preopercle's posterior free margin rises at a general angle to the

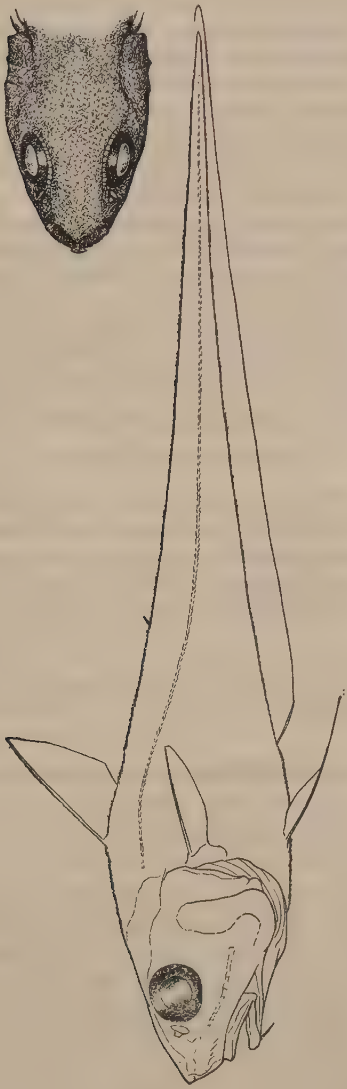

Figure 19.—*Cariburus mexicanus*, n. sp., with dorsal view of head.

horizontal of about 75°, with distinct backward curvature toward the broadly rounded lower corner. Suboperculum not emarginate. Upper branchiostegal completely hidden. Interoperculum projects conspicuously beyond lower corner of preopercle to the same vertical as lower posterior corner of subopercle. Fleshy free margin of outer opercular cover with a slight, but distinct, fold or indentation between subopercle and interopercle. Exposed part of interopercle with normal pigmentation, but without scales. 8 tubercular gill rakers on lower limb of second arch. First gill slit reduced, 5–7% of head.

Fins. Bases of pectorals slightly in advance of origin of 1st dorsal, the ventrals conspicuously behind pectorals, below, or slightly behind, origin of 1st dorsal. Fins moderate. Base of 1st dorsal about 25%, its height about 70%, of head; snout to 1st dorsal fin about 15% longer than head. Origin of 2nd dorsal far behind origin of anal fin, which is considerably behind end of base of 1st dorsal. Anterior rays of 2nd dorsal minute. Distance from anterior end of ventral fin bases to origin of anal rather long, about 45% of length of head. Length of pectorals 42–50%, length of produced ventral ray 60–70%, of head.

D_1. 11 V. 10 P. 21

General Coloration. Slightly pinkish, quite light brown. One specimen darker than the rest, but otherwise indistinguishable. The narrow black rim of the orbits stands out conspicuously against the light general color. Outer branchiostegal membrane, integument between the rami of the lower jaw, and barbel light. Inner branchiostegal membrane, oral cavity, gill cavity and peritoneum black.

Size. Attains a length of 2–2½ feet.

Range. Gulf of Mexico. "Atlantis" samples: 4 spec., at St. 2836; 1 spec., at St. 2853 Q; 2 spec., at St. 2853 T.

Genus **CHALINURA** Goode and Bean, 1883

Chalinura Goode and Bean, 1883: 198; 1895: 411.
Chalinurus (subgenus of *Macrurus*) Günther, 1887: 144.
Chalinura (subgenus of *Macrurus*) Koefoed, 1927: 100.

Branchiostegal rays 6. No naked areas on abdomen. Anus at origin of anal fin, which is in posterior third of distance from ventrals to end of abdominal cavity. Less than 15 pyloric caeca. Scales on body moderate, rather deciduous; scales on back and nape always ctenoid, with spinules arranged in linear, subparallel series. Spinules on scales in ventral region often reduced, sometimes entirely absent. Tip of snout without button-like scute; lower surface of snout without scales; a scaleless area on each side above, and immediately behind, fronto-lateral edge of snout. Mouth moderate to large, upper jaws 38–50% of length of head. Less than 15 gill rakers on lower limb of second arch. Eyes small; diameter of orbits less than 25% of length of head. Posterior part of interoperculum exposed beyond corner of preoperculum in the form of a thin and narrow produced corner, which meets the lower corner of suboperculum to form a well-marked prominence in the dermal margin of outer gill cover. Upper branchiostegal ray not exposed. Dentition variable. Dorsal spine serrate. Distance from anterior end of ventral fin base to anal fin 45–55% of length of head. Ventrals with 9–11 rays, the first ray produced.

KEY TO THE SPECIES OF *Chalinura*

1a. Head compressed, interorbital width 25% of the length of head, or less. Snout low, scarcely prominent. Mouth large, lateral, subterminal. Upper jaws more than 40% of head. Eyes small, less than 20% of head. *simula*, below

1b. Head not compressed. Interorbital width 30% of the length of head, or more.

  2a. Head small. Snout prominent, pointed. Eyes moderate, 20% of length of head, or more. Mouth moderate, upper jaws 40% of head, or less. *carapina*, p. 68

  2b. Head very large and broad. Snout high, nearly vertical. Eyes very small, less than 20% of head. Mouth large, subterminal. Upper jaws more than 40% of head. *brevibarbis*, p. 71

Chalinura simula Goode and Bean, 1883

Figures 20, 9 (p. 31).

Chalinura simula Goode and Bean, 1883: 199; 1895: 412; Jordan and Evermann, 1898: 2578; 1900: fig. 910; Roule, 1919: 86; Jordan, Evermann and Clark, 1930: 204; Schroeder, 1940: 234.

Macrurus (*Chalinurus*[20]) *simulus* Günther, 1887: 145; Lütken, 1898: 27; Ehrenbaum, 1902: 117; Murray and Hjort, 1912: 398; Koefoed, 1927: 100.

Coryphaenoides simulus Fowler, 1936: 457.

General Characters. Head compressed, moderate, its length 19–23% of total length. Trunk moderate, compressed, with almost flat sides, tapering very gradually into tail; distance from snout to anal fin about 30–35% of total length, or 1.4–1.6 times length of head. Greatest depth 65–70% of head. Abdominal cavity extends beyond origin of anal fin for a distance equal to about 15–18% of head. 7 thin, simple pyloric caeca, reaching a length of more than 25% of head.

Body Scales. Almost all lost, but scale-pockets and the few scales present indicate the general features of the genus. About 16–18 scale pockets in a longitudinal row from shoulder above abdominal cavity over a distance equal to *half* the distance from snout to dorsal fin; about 23–25 over same distance along the middle of wall of abdominal cavity. Scales on flanks, *i. e.*, walls of abdominal cavity, reduced in size and nearly smooth (?); those on neck, on back down to top of abdominal cavity, as well as those on entire tail, larger, with parallel

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[20] Also spelled *Chalinura*.

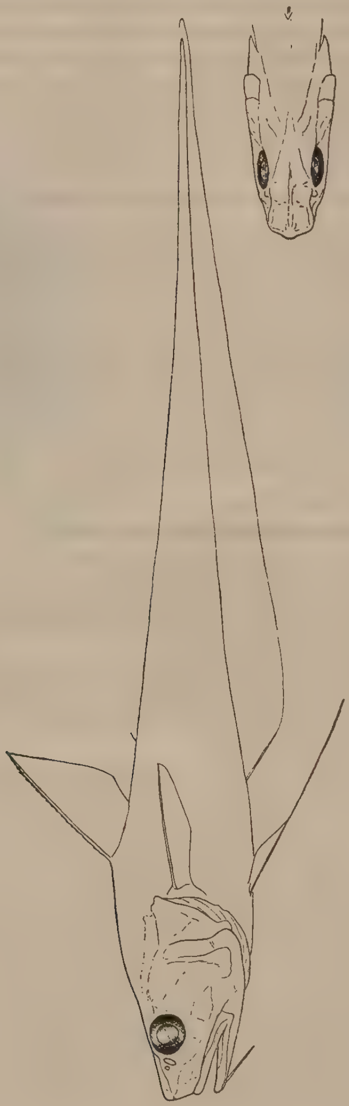

Figure 20.—*Chalinura simula* Goode and Bean, with dorsal view of head.

or slightly diverging rows of short, few and closely-applied spinules present as in the other species.

Head Scales. Since only a few scales remain on any of the specimens, it is impossible to give a description of the squamation of the head. It seems quite clear, however, that there are no scales in the entire region below the snout, or between the lower edges of the suborbital bones and the mouth; on the other hand, the lateral and dorsal surfaces of the head above this area, as well as the cheeks, are generally scaly, with the exception of the paired, roughly-rectangular, lateral areas immediately behind the snout dorsally, which are apparently scaleless also. Lower surface of lower jaw evidently without scales. Point of snout without specially differentiated shield. Apparently only a single row of small scales, which form the lateral edges of snout anteriorly, separate its naked ventral surface from its naked dorsal areas, the latter being separated from each other by a single median row. The median and lateral ridges on snout are clearly marked, although not conspicuously raised. This also applies to the suborbital ridge, which is clearly in evidence, but which fails to establish a separation between a dorso-lateral and ventro-lateral surface. No other conspicuous ridges. Skin firmly attached along ridges just mentioned; otherwise closely applied but not rigidly fixed.

Head Characters. Dorsal profile of head nearly straight from neck to tip of snout. Snout rather low, scarcely prominent, rising almost vertically from upper lip, its median height 8–11% of head; definitely broadly angular in dorsal view rather than rounded, the anterior angle about 150°; length from orbits about 25–27% of head. Mouth large, subterminal and lateral. Upper jaws 42–46% of head, reaching to below posterior margin of orbit. Premaxillaries extend to corner of mouth. Barbel very thin, but fairly long, about 20–25% of head. Eyes small, lateral, subcircular or slightly elongate; diameter of orbit 17–18% of head; upper margins of orbits not indented in lateral outlines of top of head in dorsal view. Interorbital width 1.2–1.4 times diameter of orbit, 21–25% of head. Posterior free margin of preopercle rises nearly perpendicularly, at a general angle of about 80° to the horizontal. Upper portion of suboperculum not emarginate. Upper branchiostegal completely hidden. Interoperculum with a narrow backward projection which extends well beyond preoperculum and joins with the somewhat produced lower corner of suboperculum to form a prominent corner in the free margin of outer gill cover (as in *brevibarbis*), which, however, remains entire, without any appearance of a free flap. First gill slit wide, about 25% of head. About 10 short, tubercular gill rakers on lower limb of second arch.

Teeth. In lower jaw in single series, except at the symphysis, where 2–4 inner teeth may occur. Teeth in upper jaw in a band, with an outer series of 16–20 conspicuously enlarged fangs.

Fins. Pectorals conspicuously in advance of 1st dorsal fin; ventrals directly below, or very slightly in advance of, pectorals. Origin of 2nd dorsal well behind origin of anal, which is only a short distance behind end of base of 1st dorsal. Fins moderate to small. Base of 1st dorsal fin about 26–29%, its height about 70%, of length of head; snout to 1st dorsal 15–20% longer than head. Anterior rays of 2nd dorsal very small. Distance from anterior end of ventral fin base to origin of anal rather long, 45–50% of head. Length of pectorals 57–63%, produced ventral rays 85–105%, of head.

D_1. 10 V. 9 P. about 18

General Coloration. Specimens all faded, so external pigmentation cannot be described. Oral cavity, gill cavity and peritoneum dark.

Size. Reaches a length of about 2½ feet.

Range. Both sides of North Atlantic in warm waters.

Chalinura carapina (Goode and Bean, 1883)

Figures 21, 9 (p. 31).

Coryphaenoides carapinus Goode and Bean, 1883: 197; 1895: 404, pl. XCVII, fig. 339; Günther, 1887: 138, footn.; Jordan and Evermann, 1898: 2579; 1900: fig. 911; Jordan, Evermann and Clark, 1930: 205; Gregory, 1933: 383, fig. 262; Fowler, 1936: 1246, fig. 535; Schroeder, 1940: 235.

Macrurus carapinus Koefoed, 1927: 107.

Koefoed (1927) first recognized that this species has its place among the members of *Chalinura* (treated by him as a subgenus), and the same conclusion is arrived at by the quite different system of generic diagnosis used in the present report. *Ch. carapina* differs from *Coryphaenoides* by all the features given in the generic key on page 22. However, it also differs from the other two western Atlantic species of *Chalinura* by the entire, typically macrouroid shape of the head with its prominent, pointed snout and by several other features. In spite of the diversity thus introduced in the genus by the inclusion of this species, it remains a well defined group, particularly on the basis of squamation. Only a very few scales are preserved on the specimens seen by the writer, but these show quite plainly the basic features of the scales of the genotype; the spinules occur only as closely applied points on low, parallel ridges, which represent a degeneration of the type of scale found in *Ch. brevibarbis* carried one short step further than in *Ch. simula*. The scales seen by the writer and herein illustrated were taken from the lower flanks. Goode and Bean (1895: 405) probably obtained scales from more dorsal locations and describe them as "showing several parallel ridges composed of small spines and rather large." This description obviously bridges the gap left in the comparison between the scales of *Ch. carapina*, and those of *Ch. simula* shown in Fig. 9, p. 31.

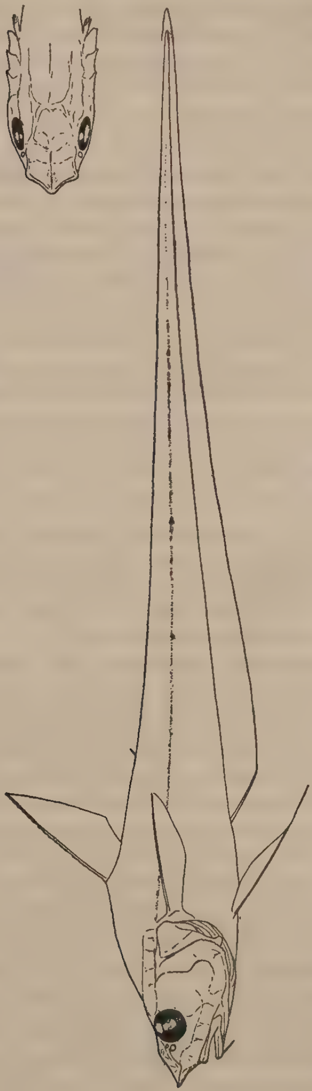

Figure 21.—*Chalinura carapina* (Goode and Bean), with dorsal view of head.

General Characters. Head relatively small, but rather broad; its length only about 16–17% of total length of complete specimens. Trunk moderate, distance from snout to anal fin about 26% of total length, or 1.5–1.6 times length of head. Greatest depth about 75–80% of head, 12–13% of total length. Tail strongly compressed. Abdominal cavity extends beyond origin of anal fin for a distance of about 15% of head length. 9 simple, short and thick pyloric caeca.

Body Scales. Only a few scattered scales preserved in any of the specimens. Although an actual count cannot be made, it seems indicated that there would be normally around 30–35 scales in a longitudinal row occupying a distance equal to that from snout to 1st dorsal fin. Scales on back and on entire tail with diverging linear rows of small spines; scales on walls of abdominal cavity with reduced spinous armature, many entirely smooth.

Head Scales. Due to the extensive loss of scales in all specimens examined, it is impossible to be entirely definite in the description of the squamation of the head. It is evident that the entire lower surface of snout anterior to the orbits is naked, and that there is also a pair of fairly large lateral naked areas immediately behind snout above, as in *Ch. brevibarbis.* On the other hand, scales are found to be present in the lower region of the area between orbit and mouth; also on the posterior parts of the ventral surfaces of the rami of lower jaw nearly to the middle of the length of the jaw; thus, the naked areas above and below the mouth are entirely discontinuous, not confluent as in *Ch. brevibarbis.* The median and lateral ridges of snout are sharp, and in general the head has a rather cavernous appearance. Suborbital ridge moderately prominent. Skin attached along ridges, but not to flat surfaces of head.

Head Characters. Dorsal profile of head strongly convex over nasal region, with a depression between orbits. Snout prominent, rather sharply pointed in lateral view, rising from upper lip at a general angle to the horizontal of about 45°; in dorsal view broadly angular, the converging lateral outlines concave, so that the point becomes rather acute, although the general angle of convergence (between tip of snout and lateral ethmoidal prominences) is about 105°; length from orbits about 30–32%, the median ventral length of snout from mouth about 18–20%, of head. Mouth rather large. Upper jaws 38–40% of head. Premaxillaries extend very nearly to corner of mouth. Barbel small and thin, about 12% of head. Eyes small, lateral, circular; diameter of orbits 21–23% of head; upper margins of orbits not indented in lateral outlines of top of head in dorsal view. Interorbital width 1.6 times diamater of orbit, 33–35% of head. Upper posterior free margin of preopercle rises at a general angle of about 60° to the horizontal; lower corner very broadly rounded and crenulate. Upper portion of suboperculum not emarginate. Upper branchiostegal completely hidden. Interoperculum with a narrow backward projection which extends well beyond preoperculum where it joins the produced lower corner of the suboperculum to form a prominent corner, but not a free flap, in the free margin of outer gill cover.

First gill slit moderate, about 20% of head. 10 tubercular gill rakers on lower limb of second arch.

Teeth. In both jaws in bands; outer teeth in upper jaw only very slightly enlarged or subequal with the rest.

Fins. Pectorals conspicuously in advance of 1st dorsal; ventrals slightly in advance of pectorals; origin of 2nd dorsal well behind origin of anal fin, which is distinctly behind end of base of 1st dorsal. Fins moderate. Base of 1st dorsal about 25%, its height about 80%, of head; snout to 1st dorsal about 25–30% longer than head. Anterior rays of 2nd dorsal fin small. Distance from anterior end of ventral fin base to origin of anal fin rather long, 50–53% of head. Length of pectorals about 70%, produced ventral rays 85–90%, of head.

D_I. 10 V. 11 P. about 18–19

General Coloration. All specimens faded externally. Oral cavity, gill cavity and peritoneum black.

Size. Probably does not exceed 18 inches in length.

Range. Both sides of North and Central Atlantic.

Chalinura brevibarbis Goode and Bean, 1895

Figures 22, 9 (p. 31).

Chalinura brevibarbis Goode and Bean, 1895: 413; Koefoed, 1927: 105, figs. 36–37, pl. V, fig. 10; Jordan, Evermann and Clark, 1930: 204.

General Characters. The general appearance of this species is dominated by the bulkiness of the broad and deep head, rather than by its length. Head moderate, about 20% of total length. Trunk fairly short, distance from snout to origin of anal fin about 1.5 times length of head, or about 30% of total length. Tail tapering rather rapidly from the trunk. Depth of body 80% of head, 15–16% of total length. Abdominal cavity extends beyond origin of anal fin for a distance equal to about 10–15% of head. 10 pyloric caeca (*fide* Koefoed, 1927: 107).

Body Scales. Nearly all lost, except in mid-dorsal region, but a couple picked from the flanks of the abdominal cavity indicate that the scales in these areas are much smoother than those on other parts. About 32–36 scales in a longitudinal series from shoulder over a distance equal to that from snout to 1st dorsal fin. Dorsal scales with 30–40 rather closely applied spines arranged in extremely regular subparallel series, appearing to the unaided eye as a very conspicuous pattern of striations. The conspicuousness of the serial arrangement on each scale is emphasized by the fact that the series are not in alignment from scale to scale; thus a patchwork effect results.

Head Scales. Morphologically uniform, with only the single row forming the lateral anterior edge of the snout differentiated from the others by form and linear arrangement. Entire region below snout scaleless, as well as between

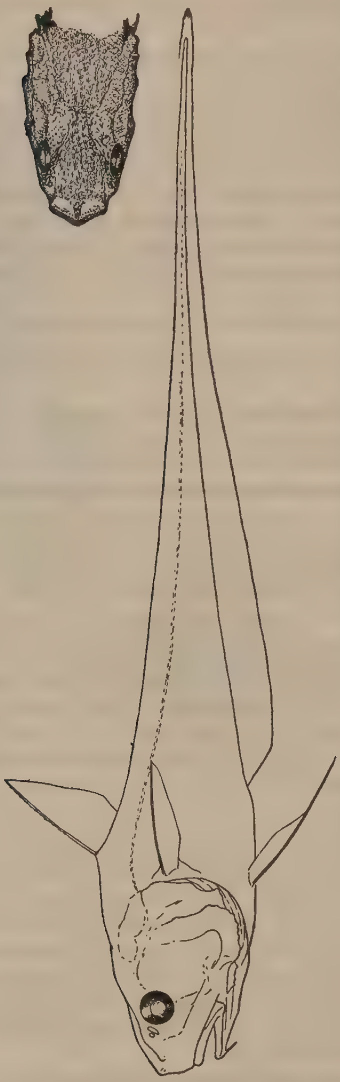

Figure 22.—*Chalinura brevibarbis* Goode and Bean, with dorsal view of head.

mouth and lower edge of suborbital bones. Entire ventral surface of lower jaw also without scales, but some uncertain markings suggest the possibility that a short and narrow band of rudimentary scales may have been present on lateral surface of lower jaw at corner of mouth. A pair of very wide but short naked areas above snout, separated from each other by a tapering band of scales (not a single linear row) in the median. Scales on head in general distributed with a conspicuous lack of well defined patterns, which is emphasized by the resulting irregularity in the orientation of the spiny ridges on the individual scales. The head shows a general tendency towards a slightly cavernous appearance, although the externally conspicuous ridges are not greatly raised. The suborbital ridge and the lateral ridges of the snout are quite conspicuous, the parietal ridges on the postorbital part of the skull moderately so on a shrunken specimen, but possibly not observable in fresh material. The skin does not appear to be rigidly fixed to the bones, except at the point of the snout, although there is, of course, a fairly close attachment along the suborbital bones. The skin in the scale-bearing median line behind the snout above is definitely loose in relation to the bones.

Head Characters. Dorsal profile steep at nape, flat at neck, concave above orbits, generally rather rugged and irregular. Snout rather high, nearly vertical, broad and blunt, its height to tip about 16% of head; in dorsal view broadly angular, with an angle of about 135°, its width between lateral corner 27–28% of head; length from orbit about 28% of head. Mouth large, subterminal. Upper jaws about 44–45% of head. Premaxillary extends to corner of mouth. Barbel small and thin, 8–10% of head. Eyes small, circular, lateral; diameter of orbit about 16% of head, its upper rim forming only a very shallow emargination in the lateral outline of top of head in dorsal view. Interorbital width very great, about 30–32% of head, nearly twice the diameter of orbit. Posterior free margin of preopercle rises at a general angle of about 65° to the horizontal. Upper portion of suboperculum not emarginate. Upper branchiostegal completely hidden. Interoperculum with a narrow backward projection, which extends well beyond preoperculum to join with a narrow downward and backward extension of suboperculum to form a prominent corner in the free margin of outer gill cover, which, however, remains entire. First gill slit strongly restricted, only about 16% of head. 10 ridge-like gill rakers on lower limb of second arch.

Teeth. In lower jaw in a single series, moderate; upper jaw with a scattered band of small teeth and a wide-set outer row of enlarged fangs.

Fins. 1st dorsal fin well behind, ventral fins slightly in advance of, pectorals; origin of 2nd dorsal only a relatively short distance behind origin of anal fin, which is a slightly greater distance behind end of base of 1st dorsal. Fins moderate to small. 1st dorsal base about 25%, its height about 60–65%, of head; distance from snout to 1st dorsal 10–15% longer than head. Anterior rays in 2nd dorsal relatively well developed, small, but not minute or rudimentary. Distance from anterior end of ventral fin base to origin of anal long, 50–55% of head. Length of pectorals about 55%, produced ventral rays about 75–80%, of head.

D_1. 9 V. 9 P. 19–20

General Coloration. Indeterminable on the available specimen. Edges of lips, oral and branchial cavities, and peritoneum dark.

Size. Less than two feet in length.

Range. Both sides of North Atlantic.

Genus **CORYPHAENOIDES** Gunnerus, 1765

Coryphaenoides Gunnerus, 1765: 50.

Head compressed, deep. Branchiostegal rays 6. Trunk very short; distance from snout to origin of anal fin less than 40% longer than head. Tail very long, 75–80% of total length. Anus at origin of anal fin, without surrounding naked area, or scaleless areas preceding it in the mid-ventral. Pyloric caeca fairly numerous, about 30 or more. Scales on body moderate or small, with long spinules in diffuse arrangement. Scales on head uniform, covering all parts, including ventral surface of snout; no modified series or naked areas anywhere. Snout very high, moderately prominent, with a button-like sculptured shield at tip. No externally visible ridges on head. Mouth fairly large. About 15 or fewer gill rakers on lower limb of second arch; all small, tubercular. Eyes large, lateral. Preopercular margin oblique. Suboperculum not emarginate. Interoperculum projects far beyond preoperculum which is enclosed in a free, fleshy flap. Teeth in bands in both jaws. Dorsal spine serrate. Anterior rays of 2nd dorsal fin reduced. Origin of anal fin advanced, far forward of origin of 2nd dorsal, barely behind base of 1st dorsal fin. Origin of anal fin approximately at, or before, middle of distance from ventrals to end of abdominal cavity. Distance from ventrals to anal fin about ⅕ of length of head or less. 8 ventral rays, the outer one greatly produced.

Coryphaenoides rupestris Gunnerus, 1765

Figures 23, 24.

Coryphaenoides rupestris[21] Gunnerus, 1765: 50, pl. III, fig. 1; Collett, 1875: 131; 1880: 70; 1885: 95; Winther, 1880: 36; Day, 1880: 335, pl. XCIII; Jordan and Gilbert, 1882: 812; Goode and Bean, 1883: 197; 1895: 402; Storm, 1884: 37; Lilljeborg, 1891: 259; Jordan and Evermann, 1898: 2579; Gilbert and Hubbs, 1916: 143; Johnsen, 1921: 48; Farran, 1924: 99, fig. 2, pl. VII, fig. 1; Jordan, Evermann and Clark, 1930: 205; deBuen, 1935: 72; Vladykov and McKenzie, 1935: 66.

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[21] The writer has followed Lilljeborg (1891) entirely in regard to earlier Scandinavian references and synonymies.

Coryphaena rupestris Müller, 1776: 43.

Macrurus (*Coryphaenoides*) *rupestris* Günther, 1887: 138; Lütken, 1898: 24; Brauer, 1906: 392; Murray and Hjort, 1912: 397; Koefoed, 1927: 91, figs. 25, 26.

Macrurus rupestris Holt and Calderwood, 1895: 455, pl. XLIII, fig. 2 & text fig.; Smitt; 1893: XXVII A, fig. 2; 1895: 590; Koehler, 1896: 494; Collett, 1896: 69; Ehrenbaum, 1902: 116; Holt and Byrne, 1910: 5; Schnakenbeck, 1926: XII, 58, fig. 21; 1931: impress. 4404, 3–31, fig.

Macrourus Stroemii[21a] Reinhardt, 1832: XIX; Sundevall, 1842: 11; Krøyer, 1845: pl. 11.

Lepidoleprus norvegicus Nilsson, 1832: 51.

Macrourus norvegicus Nilsson, 1855: 600.

Coryphaenoides norvegicus Günther, 1862: 396; 1874: 139; Lütken, 1872–73: 5.

General Characters. Head moderate to small, its length probably only about $^1/_6$ of total length of a complete specimen. Trunk very short, tapering very gradually into the strongly compressed tail; distance from snout to anal fin probably about ¼–⅕ of total length, 30–40% longer than head. Greatest depth about 80–85% of head. Head and trunk deep and compressed, with almost flat sides. Abdominal cavity, which is broadly rounded posteriorly in lateral view, extends to a vertical 20% of length of head beyond origin of anal fin. About 31 long, slender, simple pyloric caeca, ⅓–¼ as long as head.

Body Scales. Uniform, without naked fossa below, or modifications in other regions. About 46–47 scales in a longitudinal series from shoulder over a distance equal to distance from snout to origin of 1st dorsal fin. Each scale with about 70–100 long, thin, erect spinules giving the outer surface a hairy texture.

Head Scales. On all surfaces morphologically uniform, without differentiation by arrangement into linear rows or other definite patterns, varying only as to size. Scales in median dorsal region of head and neck not uniformly graduated; those on neck decrease to a quite small size at occipital end of nape, those on head increase again very rapidly to a size, between posterior orbits, which is greater than that of any other dorsal scales anterior to dorsal fin; above middle of orbits there is again a rapid decrease in size to a uniform small squamation which extends without further change to tip of snout, around its sides, and backwards below orbits, where the increase towards the larger scales on cheeks is very gradual. Although the changes in the size of scales on the dorsal surface are very rapid, they do not lead to the development of definite lines of demarkation between areas of different sized squamation. Scales on posterior, upper parts of gill cover only slightly smaller than anterior scales on body between pectorals and lateral line. Conspicuously reduced scales in post-temporal region; only in a narrow band along upper edge of gill cover. Squamation of entire snout uniform and uninterrupted by naked areas either in the median

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[21a] Also spelled *Macrurus strömii.*

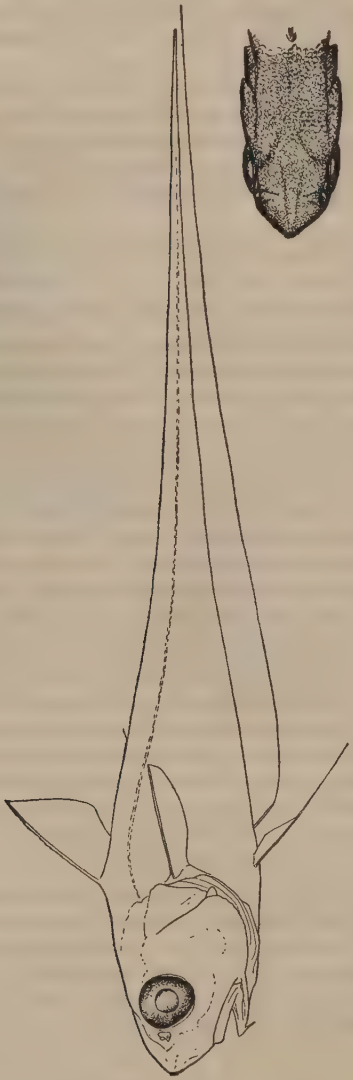

Figure 23.—*Coryphaenoides rupestris* Gunnerus, with dorsal view of head.

below, or on sides above. Lower jaw densely scaly, but gular and branchiostegal region entirely free from scales. Point of snout with a small button-shaped plate with radiating ridges. Head is of a very smooth general form, without externally visible ridges in any region. Skin on head loose and unattached to the skeleton on entire dorsal surface of skull; generally free or only quite loosely connected with the bones on sides of head. Only definite and conspicuous point of attachment is provided by the bony button at tip of snout.

Head Characters. Dorsal profile arched, with increasing convexity towards snout, and without evident concavity over eyes. Snout very high, moderately prominent, rounded triangularly in lateral view, its ventral profile rising from mouth at an angle of about 60° to the horizontal; length from orbits about 25[22]–30%, height above mouth (to point of snout) about 25%, of head. Mouth relatively large. Upper jaws about 40% of head. Premaxillaries extend to corner of lips. Barbel almost rudimentary, less than 5% of head. Eyes rather large. Orbits ovate, with the broader portion above; entirely lateral, their upper margins not indented in the outlines of head in dorsal view; lower anterior rim approximately parallel with ventral profile of snout; longest horizontal diameter of orbit about 27–31%, longest subvertical diameter noticeably greater, about 31–33%, of head. Interorbital width 36–40% of head, 1.3–1.4 times

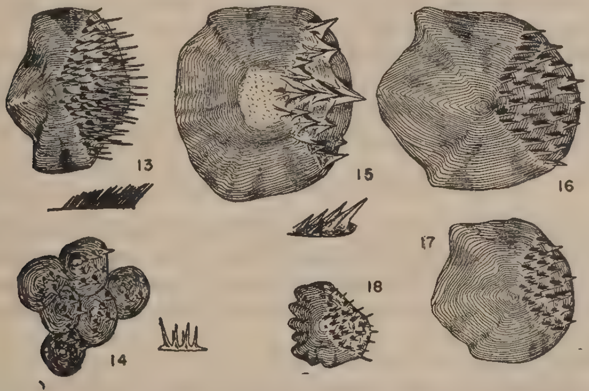

Figure 24.—Enlarged drawings of scales from flanks of: (13) *Coryphaenoides rupestris;* (14) *Trachonurus sulcatus;* (15) *Oxygadus occa;* (16) *Coelorhynchus carminatus;* (17) *C. caribbaeus;* (18) *Hymenocephalus cavernosus.*

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[22] Farran (1924: 100) gives measurements of his largest specimen indicating a length of snout of only 19% of the length of head, while the proportions of his smaller specimen agree with the material seen by the writer. The figure for the larger specimen is probably due to accidental distortion. Accidental compression of the snout is also suggested in Farran's figure.

horizontal diameter of orbit. Preopercle's posterior free margin rises at a general angle to the horizontal of about 50–55°, with a very broadly rounded lower posterior corner. Upper portion of suboperculum not emarginate. Upper branchiostegal ray completely hidden. Interoperculum projects far beyond preoperculum and also well beyond the lower corner of suboperculum, forming a free flap separated from the fleshy margin of suboperculum by a sharp fold and indentation. Interopercular flap with normal external pigmentation, but without scales. First gill slit about 10–15% of head. About 15 reduced gill rakers in the form of transverse ridges on lower limb of second arch.

Teeth. In bands in both jaws. Outer teeth in upper jaw slightly enlarged.

Fins. Origin of 1st dorsal, pectorals, and ventral fins in a straight line, with dorsal slightly in advance of, and ventrals slightly behind, pectorals. Fins moderate. 1st dorsal base about 27–28% of head, its height about 70% of head or more; snout to 1st dorsal fin less than 10% longer than head. Origin of 2nd dorsal far behind origin of anal fin, which is only slightly behind end of 1st dorsal fin base. Anterior rays of 2nd dorsal minute. Distance from anterior end of ventral fin base to origin of anal very short, about 18% of head. Length of pectorals about 60%, produced ventral ray about 80–85%, of head.

D_1. 11–12 V. 8 P. 16–18

General Coloration. A rather clear medium brown. Orbital rims, oral cavity, branchial cavity, and peritoneum dark. Gular and lower branchiostegal region with streaks of the normal brown body pigmentation along exposed folds. Outer branchiostegal membrane generally light, except for a dark area below the pectoral fin base.

Size. Reaches a length of over three feet.

Range. A northern species occurring on both sides of the Atlantic southward to the Bay of Biscay in the east and to Cape Hatteras along the American coast. Mostly in deep water (400–1200 fathoms) where it is quite common within its range, although recorded off Newfoundland at least once above 100 fathoms.

Genus **TRACHONURUS** (Günther, 1887)

Trachonurus (subgenus of *Macrurus*) Günther, 1887: 124 (in key to subgenera).

Head without externally visible ridges. Branchiostegal rays 7. Tail very long, about ¾ of total length. No lense-shaped luminous organs. Anus far in advance of anal fin, surrounded by a wide scaleless area which extends forward to bases of ventrals. Less than 20 (11) pyloric caeca. Scales small, uniform, imperfectly imbricated, each with a moderate number of long, erect spinules which lend a furry texture to skin. No enlarged scales along 2nd dorsal. Squamation covers all surfaces of head above mouth, including entire length of interoperculum, which is exposed along its lower margin and over a considerable distance posteriorly. Scales also present in converging ventral rows on gular membrane between hyoid arches. Snout moderately prominent, blunt. Mouth moderate. First gill slit restricted. Less than 15 gill rakers on lower limb of second arch. Eyes moderate. Teeth in both jaws in villiform bands, with outer series of enlarged teeth in upper jaw. Dorsal spine smooth. Anterior rays of 2nd dorsal fin rudimentary. Origin of anal fin well forward below abdominal cavity, approximately midway between ventrals and end of abdominal cavity. Distance from anterior end of ventral fin bases to anal fin about 25–35% of length of head. Paired fins very small, their lengths much less than ½ length of head.

Contains only one small, black-colored species from the Atlantic.

Trachonurus sulcatus (Goode and Bean, 1886)

Figures 25, 24 (p. 77).

Coryphaenoides sulcatus Goode and Bean, 1886a: 596; 1895: 403, 533.
Macrurus (*Malacocephalus*) *sulcatus* Günther, 1887: 149.
Trachonurus sulcatus Goode and Bean, 1895: 410, pl. XCVIII, fig. 343; Jordan and Evermann, 1898: 2591; Jordan, Evermann and Clark, 1930: 207.
Coryphaenoides asperrimus Vaillant, 1888: 229, pl. XVIII, figs. 2–2b.
Trachonurus asperrimus Roule 1919, p. 82, pl. III, fig. 2, 2a.

While the measurements of the type specimen of *T. sulcatus* show some slight differences from those of the eastern specimens described by Vaillant and by Roule under the name of *asperrimus*, the proportions of the second western Atlantic specimen[23] in the U. S. National Museum obliterates the distinction between the eastern and western representatives; therefore *asperrimus* may be regarded as a synonym of *sulcatus*.

General Characters. Head small; length about 13–14% of total length of complete specimen. Trunk small; distance from snout to anal fin 1.5–1.6 times length of head, about 22% of total length. Tail long, slender, filamentous. Greatest depth about 70–80% of head. Abdominal cavity extends beyond origin of anal fin for a distance equal to about 30% of length of head. A naked area extends from posterior end of ventral fin bases to origin of anal fin, with a wide expansion surrounding the vent, which is situated about midway in the naked area just defined. 11 simple pyloric caeca.

Body Scales. Small, firmly adherent, uniform on all parts, incompletely imbricated (with only slight overlappings); about 20 scales in a longitudinal series from shoulder over a distance equal to about *half* the distance from snout to dorsal fin. Each scale with a small number (5–10) of long erect spines, which give the skin a furry appearance.

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[23] Goode and Bean's statement about the bad mutilation of the second specimen evidently refers to the fact that the head is virtually severed from the body. The head itself, however, is undamaged, and its proportions easily measured.

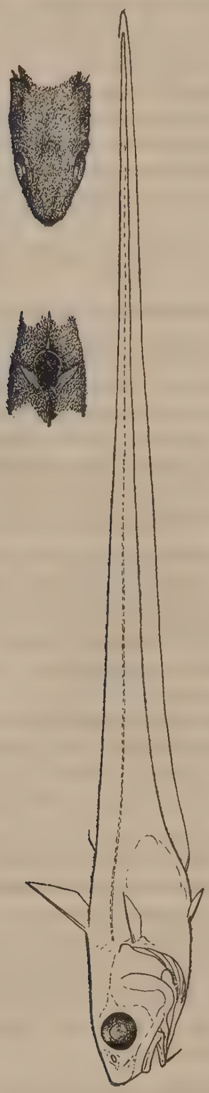

Figure 25.—*Trachonurus sulcatus* (Goode and Bean), with ventral view of anal region and dorsal view of head.

Head Scales. Uniformly covered with dense spinigerous squamation, which extends uninterrupted from dorsal surface of snout down over ventral surface to edge of skinfold surrounding mouth. Uniform squamation also covers entire cheeks and gill cover, including posterior exposed corner and inferior exposed zone of interoperculum, and extends forward over entire ventral surfaces of rami of lower jaw. A Y-shaped pair of converging ribbons of squamation also occur in gular region inside of hyoid bones. Point of snout without modified scale or scute.

Head Characters. Dorsal profile of head smooth. Snout steep, slightly prominent, rather bluntly rounded, its lower profile rising from mouth at a general angle to the horizontal of about 60–70°; length from orbits about 26%, median ventral length of snout from mouth about 14–15%, of head. Mouth moderate. Upper jaw 30–35% of head. Premaxillaries extend to corner of mouth. Barbel moderate, about 15% of head. Eyes moderate, lateral, circular; diameter of orbit about 28–30% of head; upper rims of orbits form straight lateral edges of top of skull in dorsal view. Interorbital width about equal to diameter of orbit. Posterior free margin of preoperculum forms an almost continuous curve from its anterior lower end behind corner of lower jaw to its upper end between orbit and top of gill slit; general orientation of posterior part of this curve is almost perpendicular or slightly inclined upward and backward. Suboperculum not deeply emarginate. Upper branchiostegal ray completely hidden. Interoperculum relatively very large, exposed behind the operculum posteriorly, as well as below operculum throughout its entire length. First gill slit restricted, its length 12–15% of length of head. About 7 tubercular gill rakers on lower limb of second arch.

Teeth. In both jaws in bands, with an outer series of about 12 enlarged, close-set teeth in upper jaw.

Fins. Origin of ventral fins distinctly behind origin of 1st dorsal which in turn is distinctly behind the insertion of pectorals. Fins small. 1st dorsal base about 18%, its height about 50–60%, of head; snout to 1st dorsal fin about 10% more than length of head. Anterior rays of 2nd dorsal fin small. Distance from origin of ventral fins to origin of anal very short, about 28–30% of head. Length of pectorals about 35%, ventrals about 25%, of head. Outer ventral ray not produced.

D_1. 9 V. 7 P. 16–18

General Coloration. Dark brownish black both externally and internally.

Size. Less than 18 inches long.

Range. Both sides of North Atlantic.

Genus **COELORHYNCHUS** Giorna, 1803, *sensu stricto*

Coelorhynchus Giorna, 1803: 179.

Head and trunk moderate in proportion to total length. Branchiostegal rays 6. Trunk moderate in proportion to head; distance from snout to anal fin only about 1½ times length of head, or less. Tail moderate, 60–70% of total length. Anus at origin of anal, without surrounding scaleless area. A separate depressed area of black scaleless skin (scaleless "fossa") in thoracic region, between, or anterior to, bases of ventral fins. Pyloric caeca in moderate numbers (10–20). Scales on body moderate or large, each armed with a number of moderate or long, slender, subequal spines not arranged in linear series, but in quincunx or irregular patterns. Head with strong ridges armed with modified, fixed scales. Dorso-lateral surface of head separated from ventral surface by a prominent, rigid, suborbital ridge which extends to preoperculum. Snout produced, with a scute at tip consisting of one median portion and a pair of lateral wings. Mouth small, inferior. Less than 15 gill rakers on lower limb of second arch. Posterior margin of preopercle oblique. Lower corner of subopercle rounded, not produced. Interopercle reduced and completely hidden behind preopercle. Upper branchiostegal ray exposed in the broad emargination of the posterior outline of subopercle, the exposed part of ray usually conspicuously broadened. Teeth in bands in both jaws. Dorsal spine smooth. Origin of 2nd dorsal behind origin of anal fin. Origin of anal fin in middle third of distance from ventrals to end of abdominal cavity, the distance from anterior end of ventral fin bases to anal origin being about ⅓–¼ of length of head. Ventrals normally with only 7 rays.

KEY TO THE SPECIES OF *Coelorhynchus*

1a. Snout sharply pointed, its tip simple, its lateral areas translucent in dorsal or ventral view. Distance from base of outer ventral rays to anal fin short, about ¼ of length of head. Scaleless spot between ventrals diamond-shaped.
caribbaeus, below

1b. Snout prominent, but blunt, with a 3-pronged, spiny scute at the tip and without translucent areas. Distance from base of outer ventral rays to anal fin longer, about ⅓ of length of head. Scaleless area between ventrals lanceolate.
carminatus, p. 85

Coelorhynchus caribbaeus (Goode and Bean, 1886)

Figures 26, 24 (p. 77).

Macrurus caribbaeus[24] Goode and Bean, 1886a: 594; Günther, 1887: 124, ftn. 3; Agassiz, 1880: fig. 202.

Coelorhynchus caribbaeus Jordan and Evermann, 1898: 2589; 1900: fig. 915; Goode and Bean, 1895: 401, fig. 338; Gilbert and Hubbs, 1920: 426 (in key); Jordan, Evermann and Clark, 1930: 207.

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[24] Also spelled *carribaeus*.

General Characters. Head moderate; length about 22–24% of total length. Trunk moderate, distance from snout to anal fin normally about 30% of total length, or 135–140% of length of head. Truncated tails with regenerated "caudal" fins seem fairly common; two examples are illustrated in Fig. 26. In such specimens the proportions in relation to total length are of course greatly distorted. Greatest depth of body 60–65% of head. Abdominal cavity extends only slightly beyond origin of anal fin, for a distance equal to 9–10% of length of head. The naked black fossa is diamond (lozenge) shaped, its width ⅔–¾ of its length, which is about 10–12% of length of head; its posterior half situated between bases of ventrals with the anterior half extending forward under throat. 15 simple pyloric caeca.

Body Scales. Moderate, about 40 in a longitudinal series over a distance equal to that from snout to 1st dorsal fin. Each scale with about 30 moderate spines, without conspicuous arrangement in any regular pattern.

Head Scales. Dorsal surface of snout with a quite large, oblong, naked area on each side immediately behind tip. Squamation along rim of orbit interrupted between eye and nostril, leaving the edge of orbit soft in this area. Ridges on head moderate, their scales not keeled, but profusely spiny and fairly distinctly set off from the other scales. Median rostral ridge, which extends slightly beyond anterior margins of orbits, becomes more conspicuous than in the other species, due to semi-transparency of snout, against which the ridge stands out as a dark bar. The paired frontal ridges on top of head divide towards the posterior end of skull, forming one pair of edges which converge to a point at nape of neck and an outer pair which diverge toward sides of neck. The lower surfaces of snout, cheeks and lower jaw entirely covered by scales, except for a narrow, lanceolate naked area extending in the median from below tip of snout to mouth. Posterior scales below suborbital ridge of normal size, anterior scales below snout minute. Scales on posterior dorsal surface of skull in post-temporal region, and on gill cover, generally as large as, or larger than, anterior scales on body. Even the most posterior scales in post-temporal region only slightly smaller than anterior scales on body. Scute at tip of snout arrow-shaped, with median portion produced and lateral wings receding.

Head Characters. Dorsal profile concave anterior to eyes, nearly straight from eye to 1st dorsal fin. Snout prominent and pointed; its ventral length about 33%, its length from orbit about 38%, of length of head; width at anterior margin of orbits equals ⅔ of its length; its lateral edges rather gracefully arched in dorsal view, converging anteriorly at an angle of about 75°; tip of snout simple, projecting beyond the point of convergence of lateral outlines; lower profile concave anteriorly, convex towards upper lip. Mouth very small; length of upper jaws about 25–28% of length of head. Premaxillaries reaching to corner of mouth. Barbel small and thin, about 12% of head. Eyes moderate, somewhat elliptical; vertical diameter of orbit equals about ⅘ of its horizontal diameter, which is

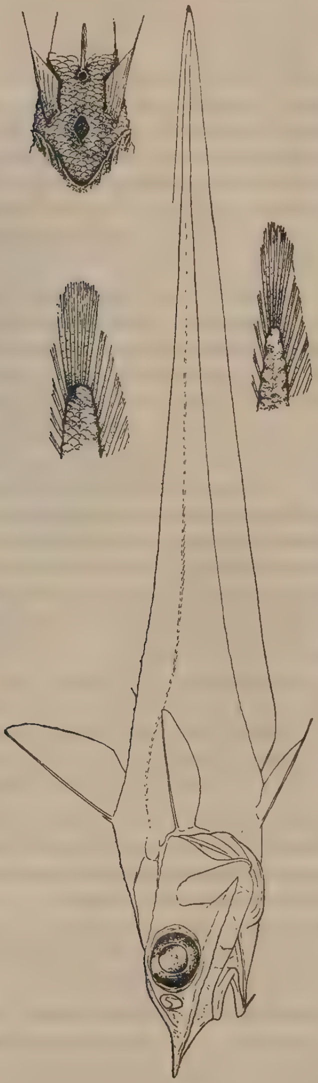

Figure 26.—*Coelorhynchus caribbaeus* Goode and Bean, with ventral view of anal region. Truncated tails of other specimens with false caudals (above and below) placed at proper distances from snout of fully drawn specimen to indicate full length of specimens with mutilated tails.

about 28–30% of head. Interorbital width ⅗ of horizontal diameter of eye, or 18% of length of head. Posterior free margin of preopercle, which slopes at an angle of about 70°, is almost straight, without conspicuous backward (concave) curvature toward its posterior corner. Lower wing of subopercle broad, laminar, forming a rounded curve parallel with lower corner of preopercle beyond free margin of latter. Upper branchiostegal ray visible in emargination between upper and lower wing of subopercle. Membranous margin of outer gill cover entire. First gill slit 15–20% of head. 9 short, tubercular gill rakers on lower limb of second arch.

Fins. Bases of pectorals barely in advance of origins of dorsal and ventral fins, which are approximately in the same vertical. Fins moderate. Base of 1st dorsal about 20–23%, its height about 40%, of head, or more; snout to 1st dorsal fin about 10% longer than head. Origin of 2nd dorsal a considerable distance behind origin of anal, which is approximately opposite the end of the base of 1st dorsal. Distance from anterior end of base of ventral fin to anal fin short, about 26% of length of head. Produced ventral ray about 50% of head, pectorals slightly longer.

D_1. 11 V. 7 P. about 15

General Coloration. Light to dark brownish grey. A black streak in and above axis of pectoral fins. Branchiostegal membrane and lower surface of head, including integument between rami of lower jaw, brownish black. Barbel white. Oral cavity light. Gill cavity and peritoneum dark.

Size. Less than 18 inches long.

Range. West Indian region. Gulf of Mexico. "Atlantis" samples: 1 spec. at St. 2815; 5 spec. at St. 2831; 4 spec. at St. 2853F.

Coelorhynchus carminatus (Goode, 1881)

Figures 27, 24 (p. 77).

Macrurus carminatus Goode, 1881: 346; Goode and Bean, 1883: 196.
Macrurus (*Coelorhynchus*) *carminatus* Günther, 1887: 129, pl. L, fig. B.
Coelorhynchus carminatus Goode and Bean, 1895: 398, fig. 336; Jordan and Evermann, 1898: 2588; 1900: fig. 914; Bigelow and Welsh, 1925: 471, fig. 237; Jordan, Evermann and Clark, 1930: 207; Schroeder, 1931: 45; Hildebrand, in Longley and Hildebrand, 1941: 33.

General Characters. Head moderate; length about 23% of total length. Trunk moderate; distance from snout to anal fin normally about 35–36% of total length, or 150–155% of head. Greatest depth about 1.5–1.7 in head, 15% of total length. Naked black fossa lanceolate, its greatest width (which occurs in its anterior half) only about ⅓ of its length, which is only about 16% of length of head. Abdominal cavity extends beyond origin of anal fin for a distance equal to 16% of length of head. 18–20 short, simple pyloric caeca.

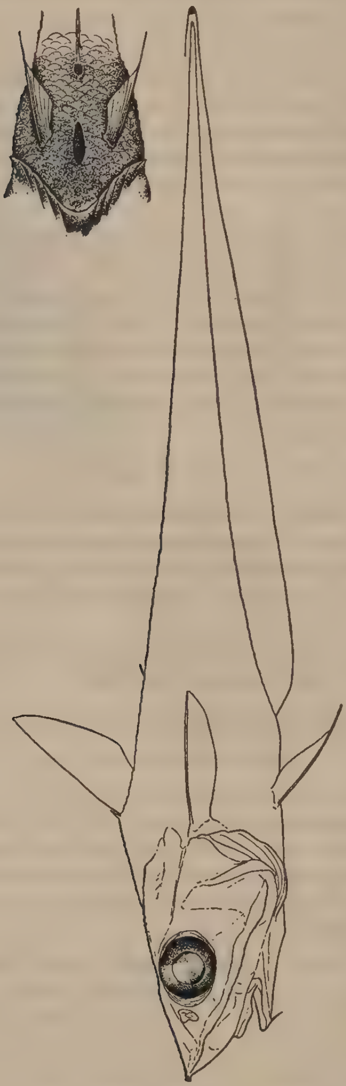

Figure 27.—*Coelorhynchus carminatus* (Goode), with ventral view of anal region.

Body Scales. Rather large, only about 30 in a longitudinal series over a distance equal to that from snout to 1st dorsal fin. Each scale with about 30 moderate spines in parallel V-shaped rows.[25]

Head Scales. No naked areas on head above suborbital ridge. Rim of orbit with continuous series of fixed scales; also between nostril and eye. Rostral areas corresponding to naked areas in *C. caribbaeus* covered with minute spiny scales. Ridges on top of head scarcely elevated at all, but recognizable by the accompanying rows of fixed scales, which are diffusely spiny without keels. Frontal ridges (or rows) divide towards nape of neck to form a pair of inner converging lines and a pair of outer diverging lines, as in *C. caribbaeus.* Lower surfaces of snout, cheeks and lower jaw entirely covered by scales, except in a narrow lanceolate median area between tip of snout and mouth. Scales on lower surfaces are of normal size posteriorly, becoming minute anteriorly below snout. Only most posterior scales in post-temporal region conspicuously reduced. Other post-temporal scales, as well as scales on gill cover and on dorsal surface of head, are of nearly the same size as anterior scales on neck and body.

Head Characters. Dorsal profile of head almost straight, with concavity above snout scarcely perceptible. Snout prominent, but relatively blunt; length from orbit about 32–33% of head; ventral length 26–27% of head, conspicuously shorter than length from orbit; width at anterior margins of orbits about 1.2 times its length; snout's lateral edges converging anteriorly at an angle of about 105° and strongly curved around the lateral ethmoids before region of nostrils; lateral wing of scute at tip of snout extended forward to form, together with the median portion, a characteristic 3-pronged bone armed with small spines on all 3 prongs; ventral surface of snout convex, both in longitudinal profile and in cross-section. Mouth moderate, upper jaws (to end of maxillary) about 30% of head. Premaxillaries very short, leaving part of upper margin of mouth, between premaxillary and end of maxillary, to be formed by a fleshy lip alone. Barbel very small and thin, 10–12% of head. Eyes moderate, somewhat elliptical; vertical diameter of orbit equals about 4/5 of its horizontal diameter, which equals about 31% of length of head. Interorbital width about 2/3 of horizontal diameter of orbit, or about 21% of head. Posterior free margin of preopercle is only slightly concave and rises at an angle of about 75°. Lower wing of subopercle broad and laminar, forming a rounded curve parallel with lower corner of preopercle beyond free margin of latter. Subopercle deeply emarginate, with upper, greatly broadened branchiostegal filling the region between upper and lower subopercular wing. Length of first gill slit about half of horizontal diameter of orbit. 9 short, tubercular gill rakers on lower limb of second arch.

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[25] Disregarding the V-shaped rows one might describe the relative positions of the individual spines as forming a very irregular quincunx pattern. But in the writer's opinion, the quincunx order is only useful and significant when developed in a very regular form. When the term is applied to the less clearly defined indications of quincunx arrangement, it merely becomes another way of stating that the spines do not form linear series in the perspective considered.

Teeth. In both jaws in villiform bands.

Fins. Origin of dorsal slightly behind, origin of ventrals considerably behind, bases of pectorals. Fins moderate. Base of 1st dorsal about 21%, its height about 55–60%, of head; snout to 1st dorsal fin about 10% longer than head. Distance from ventrals to anal fin moderate, about 32–33% of length of head. Origin of anal fin about midway between verticals from end of 1st, and from the beginning of 2nd, dorsal fin. Produced ventral ray slightly less, pectoral fin slightly more, than half the length of head.

D_1. 10 V. 7 P. about 17–18

General Coloration. Dark brownish grey. Pectoral axil, branchiostegal membrane and entire ventral surface of head brownish black. Oral cavity, as well as gill cavity and peritoneum, black.

Size. Probably does not exceed 18 inches in length.

Range. Tropical and temperate western North Atlantic, Caribbean, Gulf of Mexico. "Atlantis" samples: 4 spec. at St. 2815; 9 spec. at St. 2817; 3 spec. at St. 2853S.

Genus **OXYGADUS** (Gilbert and Hubbs, 1920)

Oxygadus (subgenus of *Coelorhynchus*) Gilbert and Hubbs, 1920: 431 (in key), 515.

Head large. Branchiostegal rays 6. Trunk large, but moderate in proportion to head; distance from snout to anal fin only about 1½ times length of head, or less. Tail short, less than 60% of total length. No lens-shaped bodies in mid-ventral line. No scaleless areas along abdomen or thorax. Anus at origin of anal fin. Pyloric caeca in moderate numbers (10–20). Scales on body moderate or large. Spines on scales strong, connected in series by high crests running between their basal portions, so that only their distal points are free. Median series and crest enlarged. Pointed scute at tip of snout; the snout very long and pointed. Dorso-lateral surface of head separated from ventral surface by a prominent suborbital ridge which extends to preoperculum. Ridges on head strong, armed with conspicuously strengthened and modified scales. Less than 15 gill rakers on lower limb of second arch. Posterior margin of preopercle oblique. Lower limb of subopercle produced into a conspicuous free flap. Interopercle completely hidden behind preopercle. Upper branchiostegal exposed in emargination of subopercle, but not conspicuously broadened. Teeth in bands in both jaws. Dorsal spine smooth. Origin of 2nd dorsal approximately above, or anterior to, origin of anal fin. Origin of anal fin about midway between ventrals and end of abdominal cavity, the distance from ventrals to anal less than half length of head. Ventral usually with only 7 rays.

Only one species in the western Atlantic.

Oxygadus occa (Goode and Bean, 1886)

Figures 28, 24 (p. 77).

Macrurus occa Goode and Bean, 1886a: 595.

Coelorhynchus occa Goode and Bean, 1895: 400, figs. 332, 333, 337; Jordan and Evermann, 1898: 2588; 1900: fig. 913; Bean, 1913: 122; Jordan, Evermann and Clark, 1930: 207.

Coelorhynchus (*Oxygadus*) *occa* Gilbert and Hubbs, 1920: 432 (in key), 515.

General Characters. Although there is no certainty that some slight regeneration at the tip of the tail may not have occurred in all specimens examined, it is evident that the species is characterized by relatively large heads (30–31% of the measured total lengths) and trunks (distance from snout to anal fin equal to about 43–45%) and short tails. Greatest depth 40–55% of head. Abdominal cavity extends beyond origin of anal fin for a distance equal to about 14–15% of length of head. 11 long, simple pyloric caeca reaching a length exceeding 25% of length of head.

Body Scales. Rather large, about 30–32 over a distance equal to that from snout to 1st dorsal fin, in a longitudinal series from shoulder. Squamation on body uniform, without naked fossa below, or modifications in other regions. Each scale with a moderate number of strong spines (12–18) arranged, and united, in series by high crests uniting their basal portions so that only their distal points are free. Among these series the median crest, with its spines, is enlarged and conspicuously dominant in the appearance of all scales. Also, on most scales there is an additional pair of enlarged crests arranged symmetrically above and below the middle series. Between these major crests a number of smaller spines occur, commonly associated with the root-like branches which divide from the main crests in the anterior region of the exposed part of the scale.

Head Scales. Entire dorsal surface of head covered by scales, without naked rostral areas. Anterior rim of orbit behind nasal area with uninterrupted series of scales. Median rostral ridge low and inconspicuous, ending between anterior ends of orbits, its scales fixed, but not keeled. All other ridges, including the entire subopercular ridge, strongly armed with fixed scales, each with a prominent, spiny keel. Tip of snout formed by a sharply-pointed, laterally-barbed, bony scute. Paired frontal ridges on top of head *diverge* slightly toward the nape of neck, *without* bifurcating; a rudimentary, separate median ridge formed by a single keeled scale often occurs between them at posterior end of skull. The supraorbital ridge continues in a straight line to top of shoulder. Lower surface of snout and of entire head is naked. In the larger specimens there are a number of irregularly-scattered, minute dermal flaps, which appear as small warts. These are scarcely perceptible in smaller examples. Squamation on dorsal surface of head merges with squamation of neck without abrupt change in size and arrangement at nape. Scales in post-temporal region and on gill cover not conspicuously smaller than anterior scales on neck and body.

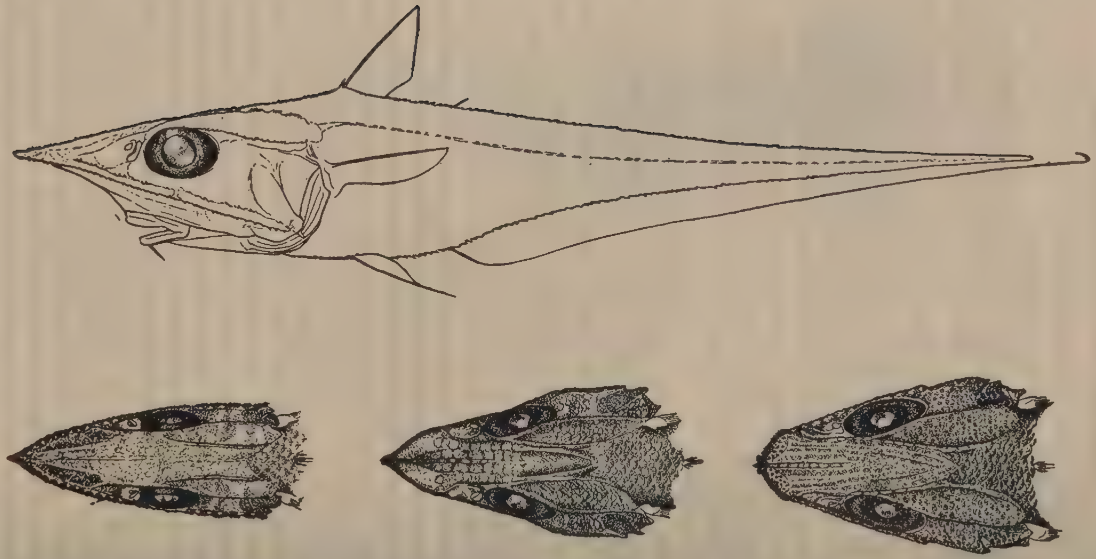

Figure 28.—*Oxygadus occa* (Goode and Bean); dorsal views of heads (left to right): *O. occa; Coelorhynchus caribbaeus; C. carminatus.*

Head Characters. Dorsal profile of snout as well as entire head nearly straight. Snout extremely prominent and sharply pointed; its length from orbits equals about 50% of total length of head in smaller specimens (heads 70–80 mm. long), slightly less than 40–45% in larger ones (heads more than 110 mm.); median ventral distance from point of snout to mouth is only slightly less than distance to orbits, or 40–46% of head; width of snout at anterior margin of orbits about ⅔ of its length. Lateral edges of snout, in dorsal view, converging as almost straight lines from the posterior end of subopercular ridge to the point of snout; general angle between the two sides only about 45°, the outlines being only slightly and inconspicuously arched in front (angle of convergence increased to about 50–55°); ventral surface of snout flat transversely and almost straight in lateral profile. Mouth very small; length of upper jaws about 25% of length of head. Premaxillaries very short, not reaching nearly to corner of mouth. Barbel small and thin, 5–7% of head. Eyes elliptical; vertical diameter of orbits only about 2.3 of their horizontal diameter, which is 22–24% of length of head. Interorbital width equal to horizontal diameter of eye, or 23% of head. Preopercular margin slopes at an angle of about 60°. Lower wing of subopercle narrow and produced into a conspicuous free flap, with the normal pigmentation of the outer skin extending downward and backward from posterior corner of preopercle, reaching across branchiostegal rays. Upper branchiostegal ray visible in emargination of subopercle, but not greatly broadened. 7–8 short, tubercular gill rakers on lower limb of second arch. First gill slit very restricted.

Teeth. In villiform bands in both jaws.

Fins. Origin of 1st dorsal fin slightly behind bases of pectorals, the bases of ventrals about same distance behind origin of 1st dorsal, and conspicuously behind pectorals. Fins small. The base of 1st dorsal about 10–16% of length of head, its height about 25–30%; snout to 1st dorsal fin about 5% longer than head. Origin of 2nd dorsal above, or slightly anterior to, origin of anal fin. Distance from ventrals to anal varies from about 30% of head in smaller specimens to nearly 40% of head in larger ones; snout to anal fin 40–50% longer than head. Pectoral length about 30% of head in smaller specimens, 40% of head in larger ones; produced ventral ray about 30–35% of head.

D_1. 9   V. 7   P. 17–18

General Coloration. All specimens seen by the writer are obviously faded, but all the evidence points to a very light external pigmentation and to a light oral cavity, but to a black gill cavity and peritoneum.

Size. Reaches a length of 1½–2 feet.

Range. Gulf of Mexico.

"ATLANTIS" STATION DATA

Station

2815. III/21/37. 29° 07′ N., 88° 16′ W.; Blake trawl; depth 285 fathoms (1800 meters wire out); trawl started down 7:20 A. M., down 7:40 A. M., started up 8:00 A. M., up at 8:30 A. M.

Coelorhynchus caribbaeus (Goode and Bean), 1 specimen.
Coelorhynchus carminatus (Goode), 4 specimens.

2817. III/21/37. 28° 58′ N., 88° 32′ W.; Blake trawl lined with material from wing of torn 20 foot trawl; 310 fathoms (2000 meters wire out); trawl started down 5:25 P. M., down 5:55 P. M., started up 6:20 P. M., up at 7:10 P. M.

Malacocephalus (*Pawnurus*) *occidentalis* Goode and Bean, 1 specimen.
Coelorhynchus carminatus (Goode), 9 specimens.

2823. III/22/37. 29° 03′ N., 88° 55′ W.; Blake trawl; depth 45–57 fathoms; down from 11:00 A. M. to 11:30 A. M.

Bathygadus vaillanti Roule and Angel, 2 specimens.
Cariburus zaniophorus (Vaillant), 1 specimen.

2831. III/23/37. 28° 37′ N., 89° 54′ W.; Blake trawl; depth 163 fathoms (1500 meters wire out); trawl started down 8:45 P. M., down 9:15 P. M., started up 9:45 P. M., up at 10:15 P. M.

Coelorhynchus caribbaeus (Goode and Bean), 5 specimens.

2836. III/24/37. 27° 48.5′ N., 89° 56′ W.; Blake trawl; depth 345–500 fathoms (2360 meters wire out); trawl started down 10.05 P. M., down 10:45 P. M., started up 11:40 P. M.

Gadomus arcuatus (Goode and Bean), 1 specimen.
Gadomus longifilis (Goode and Bean), 1 specimen.
Ventrifossa atlantica n. sp., 1 specimen.
Cariburus mexicanus n. sp., 4 specimens.

2853C. IV/9/37. Noon position: 29° 29′ N., 88° 46′ W.; Otter trawl; depth 16–24 fathoms; trawl started down 7:03 P. M., down 7:12 P. M., started up 7:33 P. M.

Steindachneria argentea Goode and Bean, 57 specimens.

2853D. IV/9/37. Noon position: 29° 29′ N., 88° 46′ W.; Otter trawl; depth 44–60 fathoms (350 meters wire out); trawl started down 8:20 P. M., down 8:35 P. M., started up 9:05 P. M.

Steindachneria argentea Goode and Bean, 14 specimens.

2853F. IV/10/37. Noon position: 29° 07′ N., 88° 43′ W.; Otter trawl; depth 43 fathoms (350 meters wire out); trawl started down 3:30 A. M., down 3:45 A. M., started up 4:15 A. M.

Steindachneria argentea Goode and Bean, 8 specimens.
Coelorhynchus caribbaeus (Goode and Bean), 4 specimens.

2853J. IV/10/37. Noon position: 29° 07′ N., 88° 43′ W.; Otter trawl; depth 51–63 fathoms (575 meters wire out); trawl started down 1:05 P. M., down 1:18 P. M., started up 1:31 P. M.

Steindachneria argentea Goode and Bean, 31 specimens.

2853K. IV/10/37. Noon position: 29° 07′ N., 88° 43′ W.; Otter trawl; depth 30 fathoms; trawl started down 4:43 P. M., down 4:50 P. M., started up 5:20 P. M.

Steindachneria argentea Goode and Bean, 56 specimens.

Station

2853L. IV/10/37. Noon position: 29° 07′ N., 88° 43′ W.; Otter trawl; depth 45–48 fathoms (400 meters wire out); trawl started down 6:05 P. M., down 6:13 P. M., started up 6:43 P. M.

Steindachneria argentea Goode and Bean, 29 specimens.

2853Q. IV/11/37. Noon position: 29° 13′ N., 87° 44′ W.; Blake dredge; depth 460–505 fathoms (1500–1750 meters wire out); started down 4:18 P. M., down 4:45 P. M., started up 5:15 P. M.

Cariburus mexicanus n. sp., 1 specimen.

2853S. IV/12/37. Noon position: 28° 22′ N., 86° 40′ W.; Blake dredge; depth 250–295 fathoms (1500 meters wire out); started down 3:40 A. M., down 4:02 A. M., started up 4:35 A. M.

Coelorhynchus carminatus (Goode), 3 specimens.

2853T. IV/12/37. Noon position: 28° 22′ N., 86° 40′ W.; Blake dredge; depth 485 fathoms (2700 meters wire out); started down 9:35 A. M., down 10:15 A. M., started up 11:15 A. M.

Ventrifossa atlantica n. sp., 1 specimen.
Cariburus mexicanus n. sp., 2 specimens.

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AN ANALYSIS OF THE DECEPTIVE RESEMBLANCES OF FISHES TO PLANT PARTS, WITH CRITICAL REMARKS ON PROTECTIVE COLORATION, MIMICRY AND ADAPTATION

By Charles M. Breder, Jr.

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American Museum of Natural History

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ABSTRACT

Fifteen genera of littoral marine fishes and two fresh water genera have been described as bearing a close semblance to various parts of plants. Except for members of three orders, all are acanthopterygians. Each genus clearly represents an independent development. Seven of the genera show resemblances to plant parts as adults and are represented by permanently small species, whereas 10 display such resemblances only when young. Eleven of these genera show similarities to floating surface objects, and only six to attached bottom growths. The resemblances of these 17 genera to plant parts are nearly equally divided between terrestrial plant parts which regularly fall into the water (9) and vegetation of aquatic origin (8).

The special resemblance of the young of *Chaetodipterus faber* (Broussonet) of appropriate size to the infertile seed pods of the red mangrove, *Rhizophora mangle*, is described for the first time. The pods are found in the sea at a time when the fish are in this deceptive state. The association of the young fish, the mangrove pods and the snail (*Cerithium*), all of about one size and all dull black as seen against a background of light sand, presents considerable optical confusion.

Three non-venomous fish that allegedly mimic poisonous fish or sea-snakes are also discussed.

As in most alleged instances of protective resemblance, the biological significance of such developments is difficult to estimate. The discussion leads to a consideration of the meaning and significance of the word "adaptation" and its current usage.

INTRODUCTION

Controversial concepts, such as "adaptation," "protective coloration" and "mimicry" and the real or fancied significance of such peculiarities to the survival of species showing them, have been the subject of many more or less analytical documents, especially in the field of entomology. However, the literature on such features as displayed by fishes is relatively scant. One possible reason is that such expressions of development and behavior are poorly represented in fishes. Another is that the comparatively great difficulty of making field observations on fishes may merely make it appear that such phenomena are rarer in this group than in the relatively more accessible insects.

Some personal observations on fishes resulted in a search through the literature for similar recorded items in order to obtain some measure of the extent of such manifestations in fishes. The present contribution is a collation of these data, with a preliminary attempt to analyze the possible significance of such phenomena in fishes insofar as the present limited data permit. As a result of this study the author is convinced that many further instances similar to those discussed will be found in nature. Furthermore, many are probably still hidden in the literature as notes which are not suggested by the titles. It is hoped that this communication may at least stimulate others to obtain and record further information from both sources. Hitherto unrecorded observations on the resemblance of a fish to a plant part serve as an illustrative example, and are discussed in detail.

The field work was carried out in 1942, under the aegis of the New York Aquarium, at a field station located on Palmetto Key, Florida. These field studies were greatly facilitated by the assistance of a local commercial fisherman, Robert Spearing. The completion of the study was performed in the Department of Animal Behavior of the American Museum of Natural History. Valuable criticisms and suggestions were given by G. E. Hutchinson, Daniel Merriman, Carl L. Hubbs, Myron Gordon, M. D. Burkenroad and Captain J. W. Atz.

Specific Resemblances to Plant Parts

Although many fishes are described as being obliteratively or protectively colored, or appear to be decorated with varied fringes or appendages which vaguely resemble vegetative parts, few have been thought of as actually resembling parts of plants in any great detail. A search of the literature has revealed but 15 genera which have been unequivocally so mentioned by various students; one additional genus is discussed herein for the first time. The following series of descriptions, arranged in taxonomic order, have been compiled with regard to "resemblance" as used in this sense.

Order Holostei

Family Lepisosteidae. In a personal communication, Carl L. Hubbs kindly supplied the following unpublished data on *Lepisosteus osseus oxyurus* (Rafinesque).

> Soon after hatching the baby gars appear at the margins of Michigan lakes' where they lie at or near the surface. They appear to be as stiff as the little twigs and the leaflets of conifers among which they float and their sooty black color matches that of the decaying wood tissue. Until they make occasional darts the baby gars are hard to tell from the plant fragments and even these actions simulate the movement of the twigs by wavelets. Although they are only one to three centimeters long the plant-simulating gars feed on newly-hatched minnows. It is possible, therefore, that the resemblance has an aggressive as well as a defensive value. Larger young lose this protective resemblance.

By way of contrast, the present author has seen similar sized young of the Florida form of *Lepisosteus* in the Everglades and at no time did they impress him as resembling any details in the environment. Here the shore litter is considerably different from that of the north woods. These young fish, while darkish in color, could not be described as black.

ORDER SYNENTOGNATHI

FAMILY BELONIDAE. The young of *Tylosurus raphidoma* (Ranzani) closely resemble short bits of plant stems. Gudger (1929) was apparently the first to mention this resemblance, which has also been observed by the author both at the Dry Tortugas and at Palmetto Key. Stems of an unidentified plant are abundant in the sea in the former locality, and the fishes resemble these closely as to form, color and size. When the dorsal fin begins to heighten and darken and the mandibular lappets appear (Breder, 1932), this resemblance largely disappears, and although the fish are still readily overlooked, they bear no great similarity to any particular plant structure.

The following notes on the behavior of a young *T. raphidoma* in the "stick-fish" stage and that of the very different *Strongylura notata* (Poey) were made at Palmetto Key. There were only one of the former and several of the latter near the end of the laboratory dock during this observation. The tide was ebbing rapidly and the drift was being swept under the dock at a fast pace, with the pieces of drift generally not more than two feet apart. The single straw-colored *Tylosurus* remained substantially in one position close to a bit of drifting stem or weed that resembled the fish in general appearance and size. As this object drifted toward the dock, but long before it passed under it, the fish darted forward and settled near another similar piece. In these movements it covered a swimming distance of approximately one and one-half feet, after which it drifted back for a similar distance before recovering its former position. The fish was about six inches long. It is not clear just what points of reference the fish used. It may have been using the dock itself, which was the nearest stationary object, although the fish was about three feet upcurrent from the dock at its closest approach. Why it selected this particular place is not evident. The whole performance may have been a method of feeding, passing from one piece of drift to another to take smaller fish or other organisms which sometimes hover under such shelter and drift with it.

In sharp contrast was the behavior of a number of *Strongylura* which remained together in a more or less loose aggregation as they kept moving about actively in an area about 20 feet in diameter. It is notable that this species is green as seen from above, not greatly different from the color of the water at this place. The *Tylosurus*, which was close to the mean size of the *Strongylura*, occasionally made movements as though to join the latter, but it never actually discontinued its association with the inert bits of trash.

These differences in the behavior of two such closely related forms may be associated with the differences in what attracts the fishes. Both are evidently impelled to draw close to objects of about their own size and color, the one associating with inert bits of plants which abound in the region, the other being attracted only to its own kind. By no stretch of the imagination are there any plant fragments to be found in this place which could be thought to look like *Strongylura*, either in form, pose or color. *Tylosurus* acts in an "inert" manner like a piece of broken plant, while *Strongylura* exhibits marked activity; this difference is apparently associated with the social attitude of the latter.

FAMILY HEMIRAMPHIDAE. According to Gilchrist (1917), the young of *Hemiramphus calabaricus* Günther, when about an inch in length, bear a most striking resemblance to broken bits of *floating* weed of the same size, which he tentatively referred to *Zostera*. Furthermore, regarding their reactions when frightened, as by a moving shadow, he wrote,

> [They] at once became rigid and floated about in any position, apparently in a quite helpless inanimate condition. They then so closely resembled fragments of weed, which also floated about, that they could with difficulty be distinguished from them, even by an observer of the transformation. This similarity was increased by the characteristic colour of these small fish, which was a dark green, very similar to that of the fragments of the weed. . . . The fish when they have assumed the rigid condition, are not easily roused from it, and can readily be caught by means of a hand net when in this state.

When they have reached a larger size and are capable of more vigorous swimming this resemblance disappears, according to Gilchrist, which, of course, it must on a basis of size alone.

FAMILY EXOCOETIDAE. Dr. Albert W. Herre of Stanford University reports in a personal communication that he has mistaken young flying fish for a flower (*Barringtonia*) floating on the surface of the sea; the species of fish was *Cypselurus nigripennis* (Cuvier and Valenciennes), and possibly *C. spilurus* (Günther) as well. He wrote,

> I was fishing by electric light, in Lembeh Strait, Celebes, and as the tide bore debris out of inlets that extended back country for many miles, I saw many blossoms of *Barringtonia* amid the flotsam and jetsam. This is a large

> tree that grows on sea beaches all over the Indo-Pacific Shores. I paid no attention to them, but after a couple of hours I was astonished as I made a dash at a little fish beside a blossom. The flower simply lifted itself out of water and flew off. Then I realized that it was a young flying fish, one of the "four-winged" kind. So after that I paid attention and secured a number of young flying fish that simulated the flower of the *Barringtonia* as they floated on the water with all their fins extended. The electric light shone upward from beneath, so that the young fish looked like, and were about the same size, as the large *Barringtonia* flowers.

These flowers are about two to three inches across. Herre doubts that this effect might obtain naturally even in brilliant moonlight. Thus it may be that the effect here described appears only under the special conditions of a submerged light; if so it would hardly be suitable for inclusion in this list. It is possible, however, that a fish, viewing either such a blossom or fish from below, would find a deceptive silhouette against a bright sky, similar but reversed to that which Herre produced with his submarine light.

The author, having collected many young flying fishes in the western Atlantic both by day and with a light at night, while aware that they are frequently difficult to recognize amid various kinds of drift, has never seen any which impressed him as resembling anything in particular, although it is easy to imagine that a floating blossom such as that described by Herre could well supply the missing element.

ORDER LOPHOBRANCHII

FAMILY SYNGNATHIDAE. Specimens of *Syngnathoides biaculeatus* (Bloch) deceived Smedley (1928) into thinking that they were the leaves of the plant *Enbalus koenigii* Richard. He wrote, "The leaves grow in twos or threes and when submerged rest at an angle of about 30°–40°"; he added that minute straggling hydroids which have the appearance of tufts of sandy hair adhere to the leaves of this plant. In describing the deception, he wrote,

> One apparent "leaf" proved on examination to be a specimen of the pipefish *Syngnathoides biaculeatus* (Bl.). On being stirred with a stick it took no notice, apparently relying on the deceptive nature of its appearance; it was indeed, some little time before I recognized its true character. . . . Its color in life was grass green with tentacular appendages of a sandy color at intervals on the ventral and lateral surfaces, helping to make the general appearance more like that of the plant.

Schneider (1900), Poulton (1908) and Luther (1912) discussed

Siphonostoma typhle (Linnaeus) and *Nerophis ophidion* (Linnaeus) resting amid *Zostera* and other plants in an imitative posture. They also discussed similar effective instances for *Syngnathus*, which seem to grade off by step-like degrees into general resemblances such as Nichols (1910) described for *Siphonostoma pelagicum* (Osbeck) in reference to *Sargassum*. Marshall (1898) mentions such resemblances in *Nerophis*.

Although many of the species of *Hippocampus* show appendages and branching growths more or less resembling the algae amid which they are usually found, no one has described them in their entirety as being easily mistaken for such a growth, in the sense here employed. In the genus *Phyllopteryx* the appendages are so extensive as to fairly hide the fish, and practically all references to this genus mention it as imitative to a high degree [see for example Günther (1865), Bouvier (1888), Vignon (1931)]. An examination of figures and preserved material certainly indicates that *Phyllopteryx* should be included in this list. The full development of this feature appears to reach its zenith in the adults where each fish, when attached by the prehensile tail, appears practically as a complete plant in itself.

ORDER SCOMBROIDEI

FAMILY CARANGIDAE. Although the young of various carangids are likely to be found swimming close to floating objects, such as driftwood or jellyfish, only one has been described as being easily mistaken for something else. Breder (1942b) so described a young *Oligoplites saurus* (Bloch and Schneider) of about 30 mm. on the mangrove coast of western Florida. The only conspicuous leaves in the water were those of *Rhizophora*. He wrote,

> They rest near the surface of the water, generally head-down or twisted in such a manner as to somewhat resemble a half water-logged leaf and present a most un-fish-like appearance. Generally they are solitary or, at most, in widely spaced groups of not more than three. In the water they seem to have the color of a yellowish leaf, but on close inspection are seen to be of a brassy silver or greenish brassy sheen. They drift motionless and allow a very close approach but are alert and quite able to dart off suddenly and can easily avoid a dip net.

One observation mentioned in the paper cited above may be of considerable significance in connection with many phenomena of this type.

> Three specimens were placed in a small aquarium which happened to contain a school of about a dozen *Harengula macropthalma* (Ranzani) [= *H. pensacolae* Goode and Bean] of similar size. Within a few hours they had become as silvery as the herrings and in a general way look somewhat like them. The transfer to the aquarium had evidently broken up their curious leaf-like drifting habit, which . . . is readily disrupted. They swam about actively in an ordinary carangid fashion and made some irregular desultory attempts at schooling with the *Harengula*, but for most part kept to themselves as a loose aggregation, never as a compact group.

ORDER PERCOIDEI

FAMILY LOBOTIDAE. Although the author has not seen any very young *Lobotes surinamensis* (Bloch), fishermen from the west coast of Florida and the coast of North Carolina have mentioned repeatedly the resemblance of these small fish to yellowed leaves. Their habit of drifting at the surface, even when large and mostly black, as discussed by Gudger (1931) and Baughman (1941), would certainly lend credence to this resemblance, to which, however, neither author made reference. Both Hildebrand and Schroeder (1928) and Beebe and Tee-Van (1928) also suggested this, the former having written,

> Young fish are sometimes marked yellow and brown. A specimen observed at Key West had the yellow and brown colors of an autumn leaf.

ORDER LABROIDEI

FAMILY POLYCENTRIDAE. This fresh-water family has produced a species which greatly resembles a dead water-logged leaf, *Monocirrhus polyacanthus* Heckel. This is a remarkable case which has been mentioned by many, including Arnold (1912), Milewski (1914 a, b), Eigenmann and Allen (1921, 1942), Norman (1931), Coates (1933) and Cott (1940). Even in an aquarium the evident resemblance is notable as to form, coloration and attitude. In the natural environment, where such objects as dead leaves are to be expected, the resemblance must be most striking. A similar, if distinct form, described as *M. mimaphyllus* Eigenmann and Allen, is essentially the same in all details of resemblance.

FAMILY LABRIDAE. The adult bright green species, *Doratonotus decoris* Evermann and Marsh [= *D. megalepis* Günther], was discussed by Breder (1925) as follows:

> The apparent irregular boundary of the dorsal, the completely transparent nature of the distal margins of the vertical fins, the entire transparence of the

> pectorals and the full coloration of the ventrals gave them in life, an extremely broken outline, so that they greatly resembled torn fragments of sea weed [*Ulva*, or a closely related form]. As they swam in the collecting pail, after the manner of their family, slowly winging their way along by means of their pectorals alone, which were perfectly invisible, and steering by their nearly equally invisible caudal, the illusion was greatly enhanced, and were it not for their irregular and erratic gyrations I might not have recognized them as fish. Even when lifted in the hand the sense of touch was called in to supplement that of vision in definitely establishing the presence of the tail fin.

ORDER SQUAMIPENNES

FAMILY CHAETODIPTERIDAE (EPHIPPIDAE). This is the only acanthopterygian family in which two genera have been noted to resemble plant parts, but these do so in very different ways.

Leaf resemblance was ascribed to yearling *Platax vespertilio* Bloch [= *P. orbicularis* (Forskål)] of two to three inches in depth from the west coast of Ceylon by Willey (1904, 1909, 1911). He wrote (1904),

> It is quite impossible to exaggerate its likeness to a leaf, and it is interesting to learn that the native fishermen also recognize the similarity by calling the fish *koskolaya* which means jak-leaf [*Rhizophora*].

His figure does not suggest a particularly good resemblance, but he evidently had the same difficulty in rendering adequate illustrations of the phenomena that the present author has also found. He wrote,

> It is a case in which a marine fish resembles, almost to the point of distraction, a faded leaf. This may appear extremely improbable, and of course it should be seen to be believed; . . . Only a carefully coloured drawing of the living fish by an artist could do justice to its wonderful form.

In addition to its physical appearance the behavior is apparently appropriate, for Willey wrote as follows in describing the capture of one in a net.

> I approached and seized the net, whereupon I saw a yellow jak leaf gently and inertly sinking to the bottom. This is surely no unusual sight close inshore, and I was about to turn away, when to my astonishment the leaf righted itself and darted away. Efforts were then redoubled and the fish secured and subsequently I sketched it alive to show as far as possible its natural contour. . . . When a fish has a leaf-shaped and leaf-coloured body and in addition has the unique habit of toppling over and feigning death when pursued, it seems natural to conclude that it is a genuine example of protective resemblance.

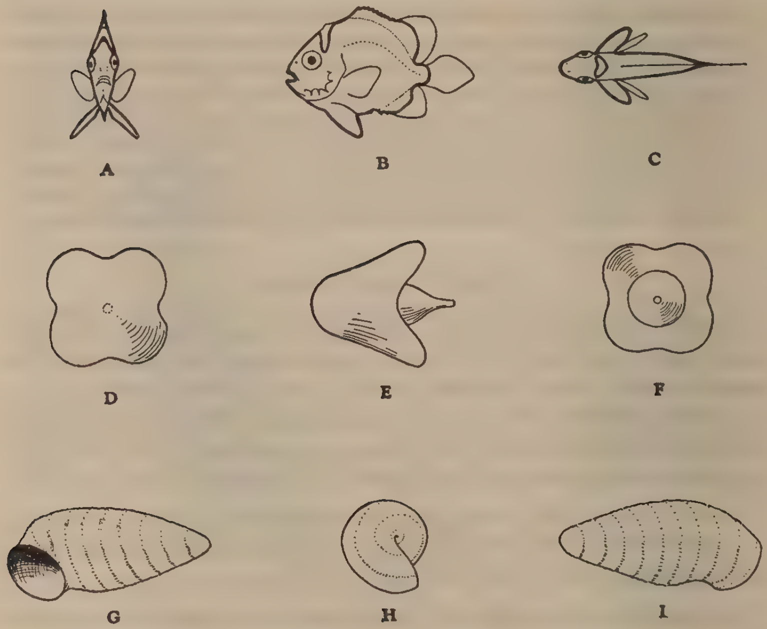

Figure 1. Diagrammatic outlines of black objects related to the concealment of young *Chaetodipterus*. *A, B, C.* Front, side and top views of a 12 mm. *Chaetodipterus.* The heavy line encompasses the black silhouette, within which the details (shown in the figures) are completely invisible in life. The dorsal, anal, caudal and pectoral fins, shown by fine lines, are completely hyaline. *D, E, F.* Proximal, side and distal views of an infertile seed pod of the red mangrove, *Rhizophora mangle.* This object, as found in the surf, is completely and uniformly dead black. *G, H, I.* Lower, oral end and top views of the snail, *Cerithium minimum negrescens* Menke. This shell is so close to being completely black that its minor markings cannot be readily distinguished without a hand lens.

Mortensen (1917) described *Platax tiera* (Forskål) in similar terms, presumably referring its similarity to the same plant.

Young specimens of *Chaetodipterus faber* (Broussonet), about 10 mm. long, are present along the clear beaches on the west coast of Florida during July and August. Although they are fairly numerous at this time, their coloration, behavior and form make finding them particularly difficult. The reasons for this are rooted in the peculiar relationship between them and their surroundings. The most striking feature in the appearance of the species in this locality, at least at sizes from about 7 to 12 mm. (standard length), is its uniform jet-black pigmentation. This extends over the body and ventral fins, but leaves the tail, posterior parts of the dorsal and anal and the pectorals absolutely hyaline and invisible under ordinary conditions. Fig. 1 a, b, and c shows this condition diagrammatically. Plate I A and B shows two fish as seen along the shore, while Plate II A represents several such specimens after they have been transferred to a white bowl. This latter plate in no way does justice to their appearance as seen in the sea. The transference to the bowl has caused several of them to show a light bar on the nape as well as other fadings, which are apparent only after they have been captured and handled. These marks are prophetic of the changes to come at a later age, in nature, when they begin passing out of the coal-black stage. On preservation these markings become even more evident.

In this connection it is interesting to note an unusual color observation in Hildebrand and Cable's (1938) excellent description of the young stages of this species which was apparently based entirely on preserved material. These authors discussed a single black specimen close to the size range at which our material normally contains individuals of this coloration, but they attributed the uniformity of pigmentation to faulty preservation. "The preserved specimen at hand is very dark, apparently having become darkened by the action of a chemical in the denatured alcohol used." This fish was 4.25 mm. long, which is smaller than our smallest. Their next larger fish was nine mm. and banded. From the present data it would appear that the specimen preserved in denatured alcohol actually held its normal color while the others had possibly faded. At least our material, both in grain alcohol and formalin, faded noticeably within a month. Earlier work on the development and life history of this species is given by Ryder (1887) and H. M. Smith (1907), but they add nothing to the details here under consideration.

In addition to not showing the intensity of the normal black pigmentation of fish in their natural environment, all the specimens in Plate II A are in poses not common to the fish in nature. The pelvic fins are folded much more closely to the body than is usual in the sea. This is in part incidental to vigorous swimming within the confines of the bowl, for the newly-caught fish are so pugnacious that they begin chasing each other and fighting almost immediately when placed together, usually damaging each other eventually. For this reason it was impossible to confine successfully more than one at a time in an aquarium. Plate II B shows individuals side-on in an aquarium.

When seen in the sea they normally spread their large black pelvics to their widest extent, which gives them a completely nonpiscine appearance, presenting at times even more extreme views than those shown in Fig. 1. In such poses they approach the sandy beaches, where they are frequently found about six inches from shore in water about an inch deep. Here they allow themselves to be rolled back and forth in the wavelets of these usually quiet inside waters. If the water becomes sufficiently rough to make a little "surf," the fishes simply move off to deeper water only to reappear when the water becomes relatively quiet again. They always pick the whitest beach available and have never been seen hovering over any of the dark bottoms which are abundant in this region. Ordinarily it might be supposed that they are especially conspicuous over the white sand; that they are not appears in the detailed description which follows.

The white sand and shell on these beaches naturally form a striking background for any black object. The small black *Chaetodipterus* are thus perfectly visible, but nevertheless they are difficult to find. Their concealment is not a matter of invisibility, but rather a confusion in the visual pattern. This results from the pepper-like distribution of two other equally black objects. At the time these fishes are in the stage described, the red mangrove (*Rhizophora mangle* Linnaeus) has finished blooming and the strange seeds still hanging on the parent tree have already sprouted, as is their habit.[1] However, there are always large numbers of seed pods which do not develop and which are presumably infertile. These fall from the trees and in a short time become a solid, dead black. Naturally many of these fall into the water and sometimes form windrows along the beaches, although they are not usually that abundant. Their actual physical form is shown in Fig. 1 d, e and f. The details as here shown cannot be seen as they float in a semi-waterlogged condition in the "surf." Outlines of them as they appear under such conditions are given in Fig. 2. Here their approximation to the appearance of the young fish is more evident. This is enhanced by the fact that both roll in the "surf" in a closely similar fashion. It should be evident that two such basically dissimilar objects bear a strikingly close resemblance when seen merely as silhouettes in the sea.

[1] Sargent (1922) wrote of this species, "Flowers produced throughout the year." Certainly on this particular island, however, there is a definite seasonal sequence in its reproductive behavior, and Davis (1940) wrote that the seedlings mostly mature during June, July and August in Florida.

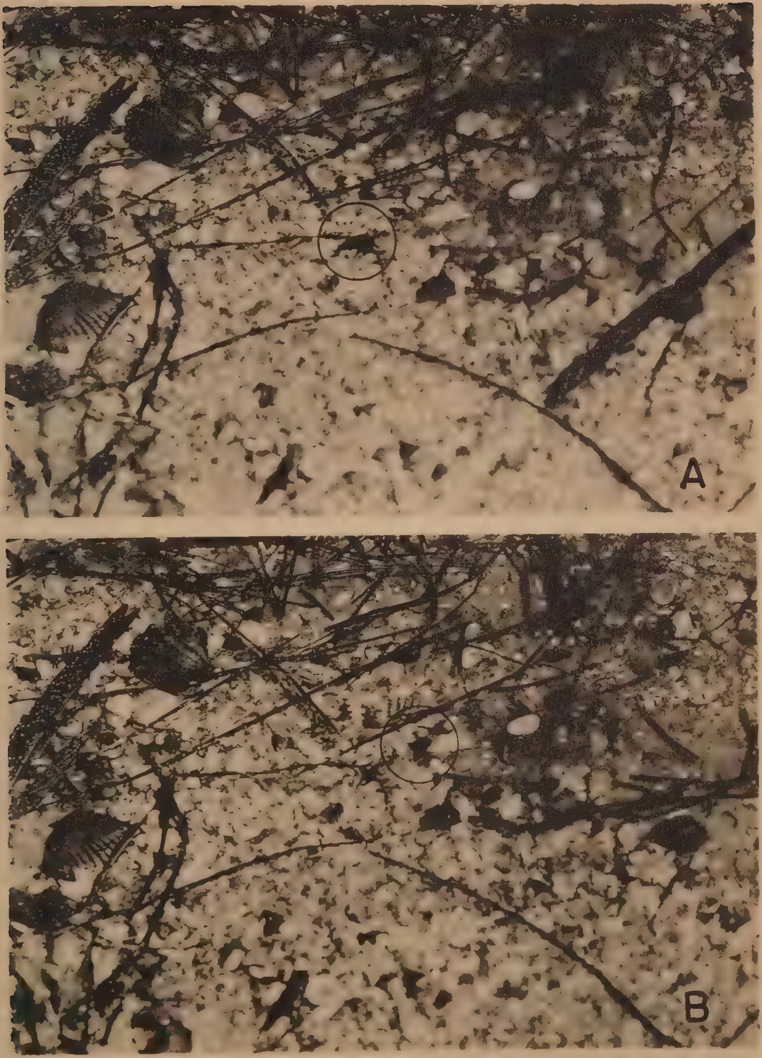

Plate I. *A*. Photograph of young *Chaetodipterus faber* (in circle) seen against the background of its normal environment. *B*. Same view a few moments later showing the fish in a different position. The snails are stationary in position and may be used as points of reference.

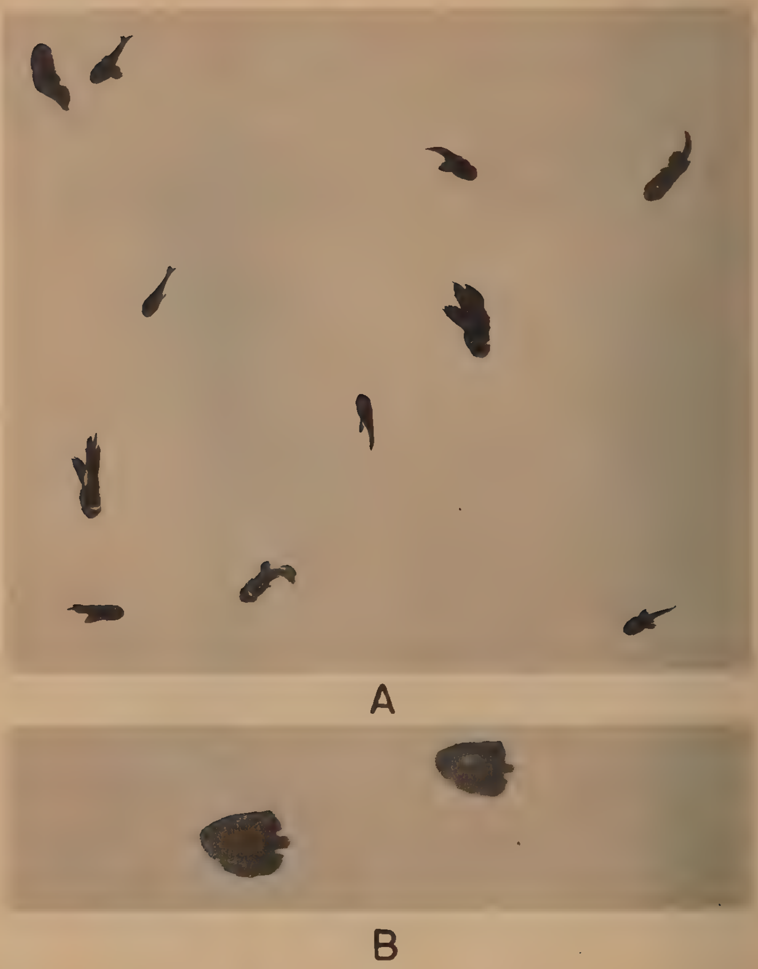

Plate II. *A*. Photographs of young *Chaetodipterus* as seen in a light-colored basin. Most of them show the white nuchal spot, a feature that becomes more intensified on capture. In the sea this spot is seldom seen, which suggests that it may result from a fright reaction. *B*. Side view of young *Chaetodipterus* as seen in an aquarium, taken with a synchronized flash, at 1/200 of a second, the fastest speed available. The poor definition is the result of their remarkable restlessness under such conditions.

The entire deception is further enhanced by the scattering of a small gastropod (*Cerithium minimum negrescens* Menke) which is always found in this association. This snail, both shell and foot, appears as black in life as the fish and pod. Its actual outline is shown in Fig. 1 g, h and i, and the silhouette in Fig. 2. For the most part these snails are attached to the bottom, crawling slowly over it. Not infrequently they lose their hold, however, and then roll for a long time before they are able to anchor themselves again. While they clearly do not resemble the fish in form, and are also somewhat larger, their greater distance from the observer reduces them to about the same size. This gives the impression of spreading the variation of form in all three objects. The optical effect is that of a white background with a peppering of small black spots of irregular outline of nearly uniform size, some of which are stationary while others are drifting aimlessly, the total effect being one that makes it difficult for the observer to determine the identity of any single item. Even after becoming cognizant of the situation it is almost impossible to be certain whether the object is a fish or a seed pod. The snails are more or less abundant throughout the year. However, there is a marked synchronization between the size, stage and habit of the young *Chaetodipterus* and the shedding of the infertile seed pods of the red mangrove. Furthermore, by the time the young fish have passed from this early stage and moved to deeper water most of the seed pods have been cast ashore by high spring tides and have disappeared as a prominent element in the "surf."

These fish clearly avoid darker bottoms which are strewn with all manner of organic debris. When the fish are frightened and pursued they pass over such areas as fast as possible and come to rest on a light colored area. This difference in bottom is evident in the photographs of Plate I A and B, which were taken at the edge of a light area so as to show both the light and dark bottoms.

A most interesting point is that *Chaetodipterus* has a greater spawning range than the natural range of the red mangrove; young fish in the stage discussed are to be found in locations other than this type of habitat. The young stages are taken on the coast of North Carolina (Hildebrand and Cable, 1938) and M. D. Burkenroad (personal communication) recalls them as not uncommon about the piling in the Mississippi Sound at only slightly larger sizes. The fact that Hildebrand and Cable found but one black specimen raises the question as

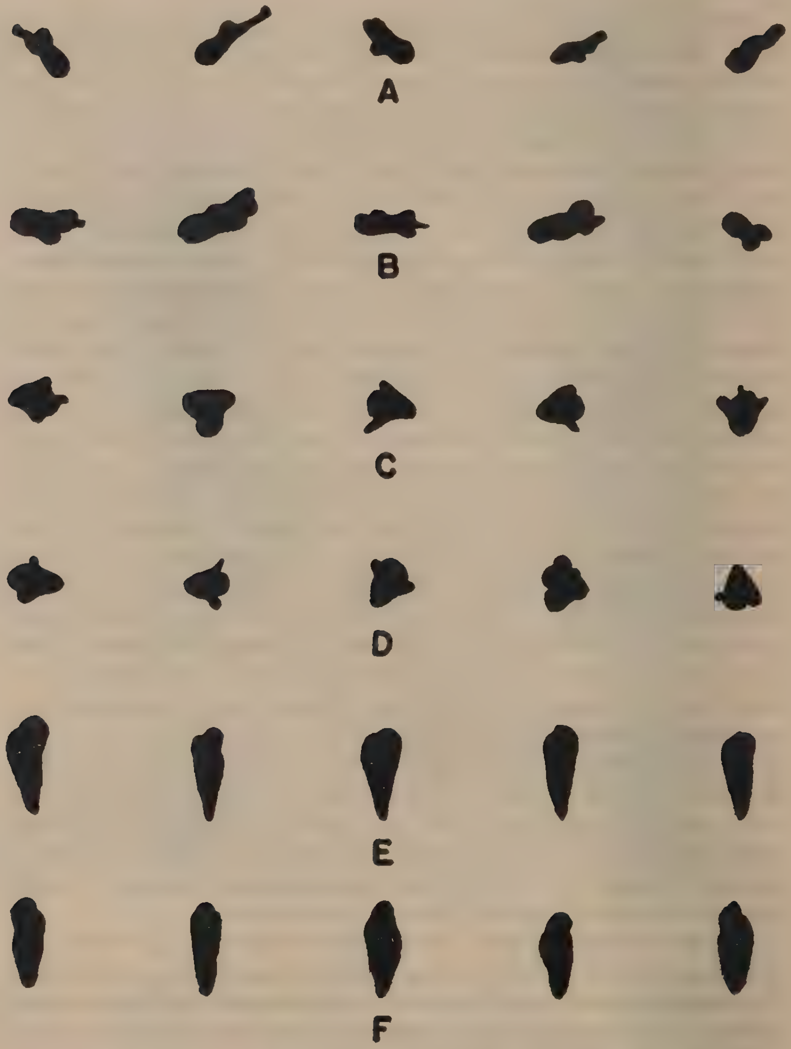

Figure 2. Black objects (life size), as seen along the shore line against white sand, traced from photographs taken for this purpose. All detail visible to the field-worker is indicated. If laid on the floor and viewed from a standing position, the normal effect is fairly represented. Rows *A*, *B*. Young *Chaetodipterus* photographed looking directly down into a bowl. These outlines do not resemble the other objects as well as do the fish in a natural habitat, because

to whether this fully black phase is commonly complete only in the mangrove areas. The possible significance of this point is treated in the Discussion.

ORDER SCORPAENOIDEI

FAMILY CYCLOPTERIDAE. After discussing the similarities of some fishes to their environment, together with their hiding proclivities, W. A. Smith (1893) wrote as follows concerning *Cyclopterus lumpus* Linnaeus.

> Perhaps the simplest and most interesting examples of such imitation is to be found in the young of the lumpsucker, *Cyclopterus lumpus*, a little greenish-blue creature without any great activity. Besides its similarity in colouring to the olive-green seaweed amongst which it dwells, I have been struck with its protective similarity in another direction. At low water on Loch Creran I have seen the young in multitudes, when the capsules were being thrown from the seaweed, hovering about these, and making no effort to escape, further than dodging along side one of the capsules which was the exact counterpart of itself, both in size and general tone of coloring. It required a very sharp eye to note the difference; and, indeed when some scores were mixed up together, it became next to impossible to distinguish the living fish from the Alga. Their movement was a quick jerk, and then quiet, when moving from point to point.

Smith accompanies this description with a rather convincing line-cut of the fish and the capsules. Unfortunately it is not clear just what species or vegetative structure is referred to as a "capsule," nor has it been possible to further identify this item. Clearly this resemblance most nearly approaches in principle that of *Chaetodipterus* to *Rhizophora* seed pods. The plant parts involved are perhaps roughly analogous and appear in the water for only part of the year at a time coincidental with a definite young stage of the fish.

Nichols and Breder (1926) wrote as follows concerning the young of this species on the American coast.

> Off the coast of New England the surface of the green water is dotted with drifting fragments or larger masses of yellowish rockweed, frequently mixed with a little eelgrass, much as the warm blue ocean waters further east are

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handling, as well as confinement in the bowl, induces rapid swimming which makes them keep the large pelvic fins relatively folded, thus more or less "streamlining" the whole outline. Rows *C*, *D*. Abortive seed pods of the red mangrove. Rows *E*, *F*. Snails, *Cerithium minimum negrescens* Menke, which form a checkered background for the other two objects. Since they rest on the bottom and are a little further from the observer than the fish or seed pods, they appear to be about the same size. Distance perception under these conditions is vague or practically absent, and these snails merge optically with the other nearer objects.

dotted with sargassum. On the Maine coast in August it is interesting to find young lumpfish, an inch more or less in total length, hiding in this drifting weed, and to compare their concealing color with that of the mouse-fish of the Gulf Stream. Unlike the color of the mouse-fish, that of the young lump-fish, is highly variable, usually olive green, sometimes dark purplish, occasionally mottled grey. They have pale spots and bands anteriorly, usually more or less whitish or silvery and tinged with blue; such a band from the snout through the eye to the corner of the opercle, another between the eyes across the top of the head, and two short ones back of the gill cleft being pretty constant. There are apt to be pale spots on the sides, a reddish tinge posteriorly and on the fins. The eye is usually pink. If one examines details of the weed, bits will be found to match even the uniform dark purplish individuals. Possibly that this environment is with the lump-fish a temporary one, has something to do with the variety of its colors; possibly there is a greater range of color in rock than in gulf weed, and a standard low visibility pattern less possible. Bright marks, found also in mouse-fish, pelagic pipefish, and young of the yellow-jack, would seem to be an important feature in such a pattern.

ORDER PLECTOGNATHI

FAMILY MONACANTHIDAE. Only one species in this group seems worthy of inclusion in the present list, but it should be mentioned that there are a number of dubious cases which appeal to the author as being in the category of chance resemblances. Thus the author has taken the bright green *Monacanthus hispidus* with *Ulva* and the equally green *Lactophrys* sp. with *Valonia;* Gordon (1937) wrote of being deceived by young *Lactophrys*. There is the possibility that these should be included here. However, detailed reasons for their omission are presented in the Discussion.

Beebe (1928) wrote as follows regarding *Alutera* in the young elongate stage.

> One of my first observations had to do with a common triggerfish, *Alutera*, of which I had taken many specimens, but had no clue to the cause of its shape and color. The solution came quickly as I watched, for one of these triggerfish swam toward me, and turned head downward when he reached a small clump of eel-grass.
>
> He took hold of a bit of coral with his sucker mouth and immediately set both vertical fins in gentle, undulatory motion, the other fins, especially the long caudal, being furled, so that the general body shape was tapering, which, together with the mottled green color, transformed it into a sea-weed frond or eel-grass blade. Now and then the fish revolved on its base without letting go. The trigger spine, slightly elevated, conveyed the impression of a bit of shredded tissue. An additional aid in the deception was the considerable variation of color in these fish, shifting from plain dark cedar green to a mottled greyish or greenish white. . .

A figure is given showing three of these fishes standing on their heads amid a bed of *Thalassia* in the manner described. In another publication (Beebe and Tee-Van, 1928) the species in question is referred to as *Ceratacanthus schoepfi* (Walbaum).

It is interesting that in connection with the same species, under the name *Alutera schoepfi*, Longley and Hildebrand (1941) wrote as follows,

> A specimen a foot long, believed to be of this species, was seen on the flats just east of Bird Key Harbor. It "floated" head downward with snout at the bottom and "drifted" slowly along, propelled by dorsal and anal fins only. The young are common in floating Sargassum, and were found occasionally also in the waste of the tern rookery.

Specimens of various sizes have been noted feeding or apparently looking for food in this manner in the tanks of the old New York Aquarium. This association presents a questionable situation in which the individuals perhaps wander accidentally into ground where hiding is automatic; such activity is probably based on feeding or other habits. It is also evident that active predation by terns takes place when this species is near the surface, as noted by Breder (1932). Another point in this connection is that of the locomotor problems in these fishes, as discussed by Breder and Harris (1935) and by Breder (1942 a).

ORDER BLENNIOIDEI

FAMILY CLINIDAE. The species *Heterostichus rostratus* Girard has been described by Holder (1907, 1910) and Holder and Jordan (1909) as greatly resembling the kelp amid which it lives. This has been confirmed subsequently by Hubbs (1920), who wrote:

> This blenny is one of the fishes characteristic of the belt of gigantic kelp (*Macrocystis*) which, along the coast of Southern California, grows in profuse beds in about ten fathoms of water. In form and color, and even in habits, the fish so closely resembles the "leaves" of the kelp as to be scarcely distinguishable from them. The thin body has the approximate form and proportions of the kelp thalli, and the long vertical fins of the fish might pass for their crinkled edges. While not as large as the average blade of kelp, this species is much larger than any of its near relatives. The usual color developed is the counterpart of that of the kelp. These peculiarities of form, size and color, considered by themselves, might well be construed as concealing protective, but when the correlated habits of the fish are taken into account, even the most skeptical could hardly deny their protective significance.
>
> These blennies live along the great strands of kelp, one or two sometimes accompanying a plant, when, loosened from its anchorage, it floats toward

shore. The female according to Holder, constructs a nest in the kelp during the process of laying the eggs, which the male fearlessly guards. They feed upon the invertebrates (chiefly crustaceans) of the kelp, and seldom wander even a few feet from the plant. They have even been observed (first by Holder, whose observations the writer has independently confirmed) poised vertically downward about the kelp, gently swaying their bodies back and forth, as the currents wave the blades of kelp.

General Resemblances to Plant Parts

There is no hard and fast line in the division between a marked resemblance and merely a slight similarity. Mortensen's (1917) descriptions and photograph of a variety of young fishes amid bits of broken drift wood and fragments in the Bay of Panama illustrate this point.

> The resemblance of the young fishes to the wooden fragments among which they swim, simply amazing in its perfectness, must undoubtedly afford an excellent protection against sea-birds, and I should think it would be equally difficult for any enemy (fish, sea-snake or anything else) to find them from below.
>
> It is particularly noticeable that it is not one species that has adopted this habit of swimming and floating among wooden fragments. I have found several species to do this, belonging to widely different genera. By far the most numerous of them are Serranids, and these are the most perfectly disguised. Monacanthids and a species of *Tetrodon* are also among them.
>
> Also the young *Aulostoma* must be included in this type of protective resemblance; not that it looks exactly like the wooden fragments, but it looks like pieces of old withered straw, which are found in the same way among the wooden fragments. Further the young *Dactylopterus* has some resemblance to the wooden fragments, but this is not so perfect as in the case mentioned above.

None of these species is included in the present list since the fish do not bear sufficient resemblance to any specific structure to be so classified.

Various species of Pediculati, especially *Histrio* (*Pterophryne*) and *Antennarius*, have been likened to *Sargassum* or other algae. The resemblance here, although certainly deceptive, is hardly sufficient to merit inclusion in the present list under the conditions outlined in the early part of this paper. See for example Bouvier (1888), Ives (1889) and Vignon (1931). Vignon (1931) discussed resemblances to such details as the epizootic fauna of *Sargassum*, specifically mentioning *Spirorbis*, while Gordon (1938) discussed in general terms the resemblance of the fish to the totality of the weed and its inhabitants. It is possible that this form should actually be included in the list. Hubbs

(1941) discussed at some length the association of color and pattern with the environment in various species of adult fishes and in the developmental stages of others. However, the forms he mentions come under general resemblances rather than the close approximations mentioned specifically in the preceding list.

MIMICRY

As already indicated, many fishes resemble the general bottom or similar backgrounds. This widespread phenomenon has been excluded from the present discussion. Quite apart from resemblances to definite *plant* parts, there is also the matter of the supposed mimicry by fishes of other animals, including members of their own class. Here, however, the confusion with independent convergences and parallelisms is such that it is extremely difficult to isolate *bone fide* instances of mimicry. Only three cases of fishes allegedly mimicking fishes seem worthy of comment here. Moenkhaus (1895) suggested that the darters, *Etheostoma* and related genera, might derive some benefit from their general resemblance to the more spiny *Cottus*. It seems more plausible, however, to consider this a case of simple convergence in which bottom living forms in flowing water show similar developments in the same environment, including bottom matching patterns of a similar order. More convincing is the account by Masterman (1908) and Anonymous (1908) of the elongate, darkened pectoral of the sole, *Solea vulgaris* Quensel [= *Solea solea* (Linnaeus)], as a mimic of the poisonous, black-flagged dorsal of the similarly partly-buried weavers, *Trachinus draco* Linnaeus and *T. vipera* Cuvier and Valenciennes. This flounder carries its black pectoral in an erect position in a manner unlike other related species. Another account which carries some conviction is that by Whitley (1935) regarding the percoid *Antrogenys vaigiensis* (Quoy and Gaimard), which resembles the poisonous spined scorpaenid *Sebastapistes bynaensis laotale* Jordan and Seale. Other vaguer resemblances mentioned by this writer are not particularly impressive.

A possible example of a fish mimicking a reptile is found in the eel, *Ophichthys colubrinus* (Boddaert) [= *Myrichthys colubrinus* (Boddaert)], which is marked with a pattern similar to that of the sea snake, *Platurus colubrinus* Schneider. According to Schnee (1905), who figured both comparatively, these species are blue and banded with encircling dark intervals. The supposition is that the eel, which presumably behaves somewhat like the poisonous snake, derives some protection from looking rather like it in form, color and pattern. This situation could conceivably form the basis of a valuable field study.

Considered in connection with the extensive literature on mimicry, mostly entomological, it is clear that the cases of resemblances to the parts of plants discussed in the present paper are included in what Poulton (1908) called *special procrypsis.* The possible mimicries of poisonous fish or sea-snakes by non-venomous fish are referable to *pseudaposematism*, or Batesian mimicry. Instances which might be referable to *synaposematism*, or Mullerian mimicry, evidently have not been reported for fishes, but it might pay to examine the many cases of parallelism and convergence in fishes critically in this connection. It is conceivable that the eel and sea snake situation might be included in this category, or even that the snake might be a mimic of the eel, since the latter are far from defenseless and since both groups have numerous brightly colored species which no one has considered to be mimetic.

ADAPTATION

Such a discussion as the present one inevitably leads to a consideration of the commonly employed word "adaptation." This word has been used in so many ways by various authors that it has become generally unsatisfactory. The term was at least comprehensible so long as it was used to indicate a condition that was considered by the author as having arisen by some selective or other means to aid the animal in its survival. Present day extension of the word to cover practically every definable item of an organism that is involved or supposed to be involved in its ability to live at all, leads to such statements as that of Huxley (1942) in concluding his discussion of "adaptation." He wrote, "We need not continue the list: it would be almost coterminous with the data of comparative physiology and physiological ecology."

Huxley, among others, also employs such expressions as "preadaptation" and "relict adaptation."[2] "Preadaptation" is thought of as a structure, function or habit which exists but has no adaptive value, thus being either neutral or deleterious, until some environmental change fits it and it becomes of positive value to its possessor, when it becomes an "adaptation."[3] As illustrative material, Huxley stated, "The spread of man favored that of organisms preadapted to be commensal or semi-parasitic on him or his crops like house-sparrow, rat, house-martin, or 'weeds' in general." A similar example which might be included is one in which man acquires a more personal interest in such animals as dogs, canaries or guppies, which, as a result, have certainly shown a considerable geographic spread and a possible increase in number. As a part of the controlling environment, a man tending an aquarium of guppies is certainly not basically different from controlling factors in other environments. "Relict adaptations" are, on the other hand, those which are no longer useful and are thus no longer "adaptations." To this comparable comments might be made.

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[2] Webster's New International Dictionary (Second edition, 1943) gives the following definition for "adaptation." "*Biol.* Modification of an animal or plant (or of its parts or organs) fitting it more perfectly for existence under the conditions of its environment;—applied esp. to a process of evolutionary change in structure and function, in organisms of a group or race. *Adaptation* is to be distinguished from the

It would thus appear that the word "adaptation" has been so broadened as to lose exact meaning, so that unless a more restricted definition can be established it is probably best to relegate it to that class of generally unused terms which do more to obfuscate than to clarify.

In order to attempt to avoid the implied knowledge of how a condition arose, the author, among many others, has frequently used the word "specialization" for a condition in which a form differs in some particular feature from other organisms which are otherwise similar to it. According to Webster, however, this is not good usage either.[4] Aside from the fact that "differentiation" is called "adaptation" by Webster, the word might be picked out alone for non-subjective usage. However, Webster defines "differentiation" as follows: "*Biol.* Modification of different parts of the body for performance of particular

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operation of the laws of heredity, although the resulting characters may be similar." Probably no biologist would be willing to accept this in its entirety.

[3] Preadaptation, according to the same dictionary, is defined as follows. "Adaptation prior in time to some specified change or condition specif. *Biol.*, adaptation (sense 2 *b*) which predisposes an organism for a specific environment." Again, this would hardly be agreeable to most biologists.

[4] Webster defines "specialization" as "*Biol. a* Adaptation in the structure of a part to the performance of some particular function; differentiation, esp. when tending toward greatly increased efficiency in one function at the expense of most other functions. *b* Adaptation in the structure of an entire organism for life in particular surroundings, or for particular habits."

functions; specialization of parts or organs." Here one is referred back to specialization; otherwise the definition is clearly subjective. "Modification" is defined as follows: "*Biol.* A noninheritable change in an organism caused by the influence of its environment." Simpson (1944) wrote,

> . . . the concept of specialization is both complex and vague. . . for present purposes it suffices to consider specialization, not as distance from a defined primitive condition or postulated point of departure and not as intensity of adaptation, but as specificity of adaptation or inverse width of the zone of tolerance.

All of this implies that both biologists and lexicographers use these words in a strictly subjective manner. Since the whole problem is so intrinsically difficult in regard to subject matter, it is evident that the words used do not aid in clarifying the situation. Perhaps it is too late to establish acceptable definitions for these words which have become so vague and nonobjective and which have such various, though always subjective, connotations. In addition to the evident general confusion on the usage of "adaptation," as indicated above, the word is also used in still other ways. Elementary text-books frequently consider the term as a fundamental property of protoplasm, using it to mean "capable of physiological response." Physiologists use the word in connnection with sense organs as meaning "entering a state in which no further response is given." Possibly a whole new set of terms should be designed in order to adequately discuss such problems. Huxley defends his various usages as biological "shorthand" to avoid undue and cumbersome circumlocution. The present author is in agreement with this viewpoint only when there is no danger of confusion, which is certainly not the case here.

Simpson (1944) discussed at considerable length the implications of such concepts by whatever terms and meaning of terms one elects to establish; he goes far in cutting through the general fog that has come to invest the entire problem. He noted that Parr (1926) had used the expressions ". . . prospective and real functions of organism and environment." Adding to this some such term as "retrospective functions," there are thus available three terms covering preadaptation, adaptation and postadaptation, but lacking their subjective connotations. Obviously "functions," as here used, could be thought of as useful, neutral or deleterious until the specific nature of a function in any of its temporal conditions (prospective, real or retrospective) could be established.

Discussion

No matter what disposition one wishes to make of the various ideas concerning protective coloration, mimicry and the significance of such matters, it must be obvious to anyone who has done even a modicum of field work that some fishes are more difficult to see than others. Since man must be considered an enemy and predator of fishes, it seems reasonable to suppose that this fact is of some value to individual fishes which are not readily seen by him. This is true in spite of the fact that many of man's current fishing methods are not dependent on the visual perception of the object sought before capture (*i. e.*, angling in deep or muddy water, seining, dredging, *etc.*); before such mechanical aids were devised, vision undoubtedly played a much more important part in the capture of fishes by man. As a case in point, it was not until his fifth year of work at Palmetto Key that the author first became aware of the presence of the small *Chaetodipterus* herein described, and of the young leaf-like *Oligoplites*. Both species were taken the first year in sizes slightly larger than these early stages. Thus it seems established that at least one such predator, who is supposed to have some special competence in field and aquarium observation, has been successfully deceived. In fact, the whole theory and practice of camouflage is based on such considerations as is pointed out by Friedmann (1944).

Those who wish to make this a special case on the basis of differences between human eyes and those of other predators are referred to Walls (1942). Two of the chief predators with which such fish have to contend are birds and other teleosts, both of which have color vision that is approximately of the same range as that of man. Thus it follows that the retinal images of the three groups are not completely dissimilar in this respect. Other optical considerations, such as angle of vision, subjective reconstruction, *etc.*, while of varied importance to their owners, do not seem to be of great relative significance in reference to the retinal details of form and color in these groups. Undoubtedly the bird's eye is more acutely sensitive to fine discriminations, and both piscivorous birds and fishes are helped by daily practice, but on the other hand they are not endowed with a brain comparable to that of man, as Walls points out in considerable detail. Consequently, there is no valid reason for assuming that such non-human fish catchers are not also deceived to a greater or lesser extent by these devices. Cott (1940) gives extended data on the large number of similar resemblances in animals, while perhaps the most convincing experiments on the protective value of coloration are those of Popham (1942, 1944) who worked on a corixid.

It must be further borne in mind that the particular resemblances here discussed are of a very special class, and that the so-called protective resemblances of fishes are extensive and included in nearly every group. Of course it does not follow that a fish (or other animal) must bear a particular resemblance to any one thing to be difficult to find, as is carefully pointed out by Huxley (1942) and Cott (1940). It often suffices for them to resemble the general bottom or other broad items of their environment, e. g., *Lophius*, *Antennarius*, *Synanceja*, *Pterophyllum*, *Orectolobus*, and flounders generally.[5] The list of species could be greatly extended without mentioning the countershading which is exhibited by almost all fishes that are exposed to light. The forms under present discussion may be thought of as highly developed extremes of this sort of manifestation. There is probably no sharply defined break in such a series and as a consequence the list here given in Table I is of necessity somewhat arbitrary. Furthermore, it is unlikely that any two observers would agree that a particular fish resembles a plant part to an exactly equivalent degree. This would surely be based partly on the discrimination, experience and conditioning of the observer, and even more important, on the exact circumstances and environment in which the observations happened to be made [see remarks under "Order Plectognathi" (p. 18) and "General Resemblances" (p. 20)].

Clearly, then, the list of fishes in Table I is composed of forms which either actually confused this particular author or which he thinks may have been confusing to an approximately equivalent degree to other observers. That the table is not purely arbitrary, however, nor merely the whim of the compiler, becomes evident when the elements inherent in the constitution of the plant-resemblers are taken under consideration. The features that account for the deceptions which are considered suitable for this table may be broken down into separate items which, when clearly present, separate these fishes from others that merely show resemblances to the general background. The phrase "general resemblance" usually can be taken to indicate

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[5] See for example Sumner (1911), Mortensen (1917), McCulloch (1925), Norman (1931), Gordon (1937, 1938), Cott (1940), Hubbs (1941) and Whitley (1943).

Table I. List of Species Showing Alleged Protective Resemblances to Plant Parts

Species	*Age*	*Plant Part*	*First Source*
Order Holostei			
Family Lepisosteidae			
Lepisosteus osseus (Linnaeus)	Young	Twigs (Conifers)	Hubbs (in lit.)
Order Synentognathi			
Family Belonidae			
Tylosurus raphidoma (Ranzani)	Young	Leaf stem	Gudger (1929)
Family Hemiramphidae			
Hemiramphus calabaricus Günther	Young	Leaf (*Zostera?*)	Gilchrist (1917)
Family Exocoetidae			
Cypselurus nigripennis (Cuv. & Val.)	Young	Flower (*Barringtonia*)	Herre (in lit.)
Cypselurus spilurus (Günther)?	Young	Flower (*Barringtonia*)	Herre (in lit.)
Order Lophobranchii			
Family Syngnathidae			
Syngnathoides biaculeatus (Bloch)	Adult	Leaf (*Enbalus*)	Smedley (1928)
Siphonostoma typhle (Linnaeus)	Adult	Leaf (*Zostera*)	Schneider (1900)
Nerophis ophidion (Linnaeus)	Adult	Leaf (*Zostera*)	Schneider (1900)
Phyllopteryx foliatus (Shaw)	Adult	Thallus (Algae)	Günther (1865)
Phyllopteryx eques Günther	Adult	Thallus (Algae)	Günther (1865)
Order Scombroidei			
Family Carangidae			
Oligoplites saurus (Bloch & Schneider)	Young	Leaf (*Rhizophora*)	Breder (1942b)
Order Percoidei			
Family Lobotidae			
Lobotes surinamensis (Bloch)	Young	Leaf	Original
Order Labroidei			
Family Polycentridae			
Monocirrhus polyacanthus Heckel	Adult	Leaf	Arnold (1912)
Family Labridae			
Doratonotus megalepis Günther	Adult	Thallus fragment (*Ulva*)	Breder (1925)
Order Squamipennes			
Family Chaetodipteridae			
Chaetodipterus faber (Broussonet)	Young	Seed-pod (*Rhizophora*)	Original
Platax orbicularis (Forskål)	Young	Leaf (*Rhizophora*)	Willey (1904)
Platax tiera (Forskål)	Adult	Leaf (*Rhizophora?*)	Mortensen (1917)
Order Scorpaenoidei			
Family Cyclopteridae.			
Cyclopterus lumpus Linnaeus	Young	Algal "Capsule" sp.?	Smith (1893)
Order Plectognathi			
Family Monacanthidae			
Alutera schoepfi (Walbaum)	Young	Leaf (*Thallassia*)	Beebe (1928)
Order Blennioidei			
Family Clinidae			
Heterostichus rostratus Girard	Adult	Thallus (*Macrocystis*)	Holder (1907)

that one or more of the constituent items, here considered essential to the phenomenon, are absent. Eigenmann and Allen (1942) gave an interesting diagrammatic analysis of these features. It is reproduced below. Their particular use of the word "mimicry" in this connection has already been noted (p. 8).

$$\left.\begin{array}{ll}\left.\begin{array}{l}\text{Protective form}\ldots\ldots\\ \text{Protective coloration}\ldots\end{array}\right\} & \text{Protective resemblance}\\ & \text{Protective behavior}\ldots\end{array}\right\}\text{Mimicry}$$

For present purposes, however, it is preferable to carry the relevant details of such an analysis to greater refinement, a pursuit that should be extended as far as possible in the present vague stage of analysis. Such a tabulation should include at least the items given in Table II. Terms differing from those used by Eigenmann and Allen are used in this enlarged and extended tabulation in an effort to avoid subjective implications as far as possible. The terms of Eigenmann and Allen are added in parentheses where their usage is parallel to that of the present paper. Definitions and explanations of the four primary items listed in Table II follow.

1. *Color.* The colors of both fish and object must be indistinguishable at least to other animals with a color vision such as that possessed by birds and teleosts, and perhaps to animals without color vision also; except for the primates, most, if not all, mammals are among these. The agreement between fish and object must be clear in regard to all three of the following items: (a) hue, (b) saturation and (c) brightness. This implies a general ability on the part of the fishes to change color to match the immediate surroundings closely. The actual optical effects obtained by animals without color vision are complicated; before any positive conclusion can be reached much more must be known about the visual mechanisms of particular species as well as about the differences in the spectral quality of light received from fish and object by the observing eye.[6] When other light ranges (*e. g.*, ultra-violet) enter into the problem, as in the vision of at least some insects, objects which appear similar sometimes become sharply distinct. No data are known to this author regarding the sensory mechanics of predation in such large piscivorous insects as *Belostoma* or their spectral limitations of vision.

2. *Pattern.* The details of the pattern of the animal must bear a deceptive similarity to that of the object which it is thought to resemble. In this it may vary from a completely uniform surface to extremely complicated patterns. The complicated pattern is obvious; but a completely uniform surface may be considered as either the

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[6] See Walls (1942) and Judd (1943) for a discussion of this matter.

TABLE II. ANALYSIS OF ATTRIBUTES NECESSARY FOR ALLEGED PROTECTIVE RESEMBLANCES*

1. Resemblance due to COLOR a. Hue b. Saturation c. Brightness	Resemblance due to SURFACE ATTRIBUTES (*Protective coloration*)	Resemblance due to all PHYSICAL ATTRIBUTES (*Protective resemblance*)	Resemblance due to STATIC ATTRIBUTES (*Mimicry*)	Resemblance due to DYNAMIC ATTRIBUTES (*Mimicry*)
2. Resemblance due to PATTERN				
3. Resemblance due to FORM (*Protective form*)				
4. Resemblance due to BEHAVIOR (*Protective behavior*) a. Posturing				
b. Movement i. Intrinsic ii. Extrinsic				

* Parenthetical phrases indicate the usage of Eigenmann and Allen (1942).

zero or infinite degree of pattern, with "zero" being so coarse that one element of the pattern covers the entire fish, while in "infinity" the details are so fine that they produce an effect of uniformity, as in a half-tone print. The uniform pattern is represented by such fish as *Lepisosteus, Doratonotus* and *Chaetodipterus* herein discussed, while very complicated matching patterns are found in flounders, some of which have been studied in great detail by Mast (1916). Generally implied in this connection is an ability to change pattern through a considerable range with greater or lesser rapidity; this is certainly the common property of nearly, if not all, species here discussed.

3. *Form.* The visible outline must be analogous, in a geometrical sense, to the object of resemblance, both in terms of its proportional parts and in terms of absolute size. Species which merely have tabs of skin, or partial approximation to the required form are here considered only as showing general resemblances and are excluded from Table I.

4. *Behavior.* This item may be broken down into its elements as follows. (a) *Posturing.* The positions assumed by the fish must be appropriate. Such inert posturing is exhibited by *Oligoplites* and *Monocirrhus.* (b) *Movement.* Associated with posturing are actual movements which further enhance resemblances. They may be either (i) *intrinsic*, where actual muscular effort is employed for the purpose (as in *Heterostichus*) or (ii) *extrinsic*, where external influences cause movements which are not resisted by the animals (as in *Chaetodipterus*). Related to such behavior is the fact that fishes of this type regularly seek out places on which they become hidden. A clump of sargasso weed dropped into an aquarium containing a *Pterophryne* will be immediately and suitably appropriated by the fish. Mast (1916) established that flounders, despite their great ability to match a variety of bottoms, will, if given a choice, settle on a bottom most nearly matching the particular hue and pattern that they happen to be displaying at the time. Brown and Thompson (1937) showed that similar behavior as regards hue is displayed by a variety of species, mostly of the family Cyprinidae.

It is evident that all species listed in Table I partake to some extent of each of the four items in Table II. Other fishes, showing general resemblances only, are defective in one or more of these items.

Of these four primary features listed in Table II, the first two ("color" and "pattern") are, in part at least, under nervous and humoral control. Such control apparently operates exclusively through the intermediation of the eye, as is shown by the inability of a blinded fish to assume any particular pattern or color change in reference to that of its surroundings. Some fishes make changes with extreme rapidity, while others take a very appreciable amount of time to effect pronounced changes of this sort. In addition to these optically governed changes there are slower physiological changes which involve the actual voidance, additional accumulation or modification of the proportions of pigments, as has been shown by Odiorne (1933, 1936, 1937), Sumner and Wells (1933), Sumner (1939, 1943, 1944, 1945) and Sumner and Doudoroff (1943). In many or all of the fishes that show reasonably rapid changes of this sort the coming of night and the consequent failure of vision causes them to lose their resemblances to their surroundings, but these resemblances are regained with the coming of morning light. This effect has been seen many times in the field and in aquaria. Those species which respond with the most speed lose their resemblances most quickly with the coming of night, while those with more lethargic reactions generally retain at least a vestige of the resemblances to which they had last adjusted.

TABLE III. ASSOCIATION OF ALLEGED PROTECTIVE RESEMBLANCES WITH VARIOUS ITEMS OF CONDITION AND ENVIRONMENT. FIGURES REPRESENT NUMBER OF *Genera* INVOLVED IN EACH CATEGORY

Item of Classification	*Resemblance to:*				*Total*
	Thallus or Leaf	*Stem*	*Seed Pod*	*Flower*	
RESEMBLANCE TO					
Aquatic vegetation	8	—	—	—	8
Terrestrial vegetation	4	2	2	1	9
RESEMBLANCE DISPLAYED BY					
Adults	7	—	—	—	7
Young	5	2	2	1	10
FOUND IN					
Fresh-water environments	1	1	—	—	2
Marine environments	11	1	2	1	15
PHENOMENON TYPICALLY NEAR					
Surface	6	2	2	1	11
Bottom	6	—	—	—	6

"Form," or external morphology, is a matter of slow development in the ontogeny of the individual. Over this the fish certainly has no immediate control, except in the sense that erectile spines and other moveable parts may change the outline, a matter which is discussed under "behavior." Depending on whether the similarity is found in the adults or the young, form is either an ultimate development or a transient development of the juvenile form.

"Behavior" is obviously a more immediate matter than any of the others. Like "color" and "pattern" it is under nervous control, which here may involve the entire locomotor apparatus. With "form" it goes far to set the examples listed in Table I distinctly apart from the merely general resemblances, which are so common among fishes. Thus it appears that "color" and "pattern" (under comparatively slow nervous control), combined with the process of development (completely free of control by the individual) and the direct behavior pattern, unite to set certain fishes or other animals apart from some others which are not so deceptive in their resemblance to details of their environment.

Considering these especially deceptive fishes alone, it is of some interest to examine various features of their appearance as classified in Table III. Obviously these data are insufficient to treat the material in a statistical manner, but it is evident from this classification that by far the greatest number bear a resemblance to leaves or the leaf-like thallus of an alga. This is not surprising, since these are the very plant structures most likely to be present in quantities in environments suitable for fishes. Furthermore, the outline of the common lanceolate type of leaf already approximates a generalized silhouette of a fish for very different reasons—perhaps what some would call a "preadaptation." It is also evident that this phenomenon is confined to shore fishes, these being the only environments in which such leaves abound. It also appears that the resemblances divide nearly equally between aquatic and terrestrial vegetation. That the bulk of these resemblances should be manifest in marine fishes is surprising. However, a possible explanation is to be found in the fact that fragments of vegetation, if present at all, are generally so abundant in rivers and fresh-water lakes that the resemblances need be only vague, whereas in the relatively light scattering of material in the sea more definite resemblances are advantageous. Also, it may be that the answer lies in the fact that marine fishes, in a broad sense, show a greater diversity than do the fresh-water forms. Note in Table I that all the marine forms represented are of families that have few or no fresh-water representatives. It is also apparent that most of the cases occur near the water surface and that only the leaf or thallus type of resemblance is found in equal numbers at both surface and bottom. Note also that of the nine plant genera mentioned in Table I, only two have more than one fish genus resembling them; that these are *Rhizophora* and *Zostera* is not surprising.

These special plant resemblances are evidently about equally divided between adult and young fishes. Obviously only adult fishes of a small size could be involved, since they would otherwise outgrow the objects they resemble. Young fish which display such resemblances eventually grow to a size which places them outside the range of the objects to which they earlier bore a similarity. As noted previously, the little *Chaetodipterus* quickly pass from the stage of seed-pod resemblance to that of small fish which are practically identical to the adults except in size.

Examining distribution of this type of behavior in regards to phylogeny as indicated in Table I and Fig. 3, it is apparent that such behavior occurs in only three orders outside the Acanthopterygii (one genus in the Holostei, four genera in the Hemibranchii, three in the Synentognathi). Within the Acanthopterygii it occurs generically once among the more typical Percoidei, once in the Scombroidei, twice in the Scorpaenoidei, Plectognathi and Blennioidei, considered in terms of family groups. In each family that shows more than one genus, the objects to which resemblances are seen are diverse.

In considering the structural manner in which the fishes resemble certain plant parts, it becomes evident that there is no common thread of similarity running through the assemblage. Among the leaf-resemblers, the long axis of the "leaf" is found to run from head to tail in *Monocirrhus*, *Oligoplites*, *Lobotes* and *Alutera*, whereas in *Platax* the long axis of the "leaf" is at right angles to the longitudinal axis. The rest are so diverse in pattern that they cannot be compared in this fashion, since each clearly represents a new departure. It should be evident from the above, as well as from Fig. 3, that all represent independent developments, mostly as terminal or near terminal forms which have certainly come to this state through evolutionary series that managed to conduct their manner of life without benefit of this particular kind of development. Note in this connection that the living relatives of all "resemblers," save in the Hemibranchii, are not notable in resembling anything in particular

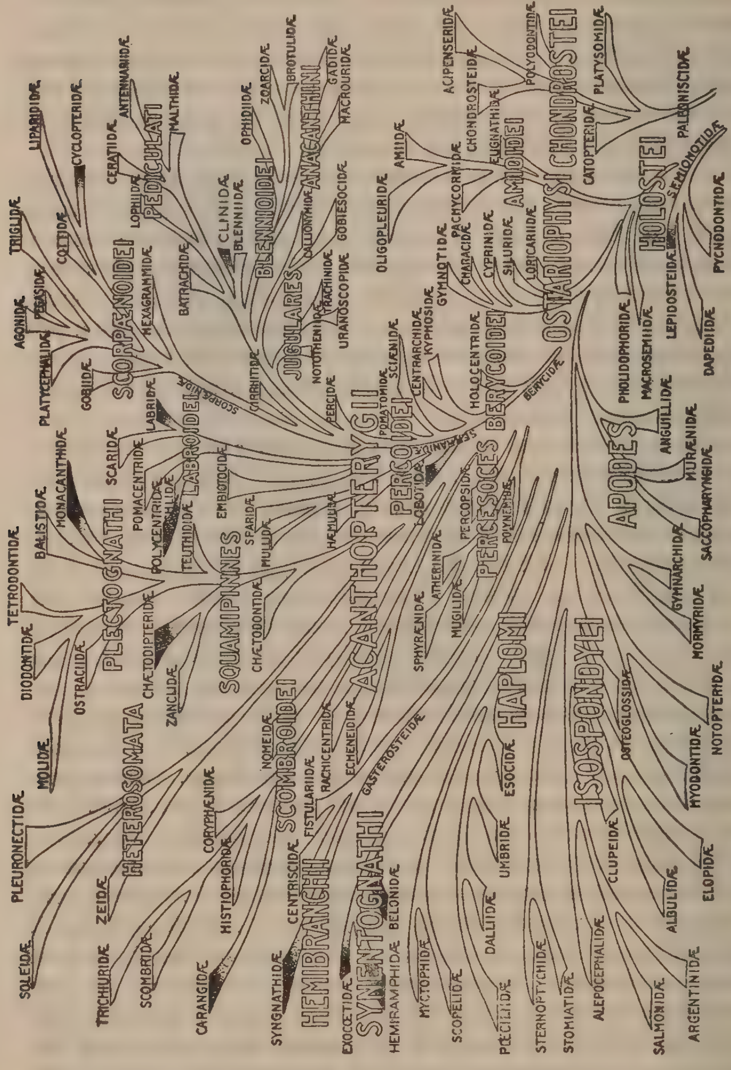
SOLEIDÆ
PLEURONECTIDÆ
MOLIDÆ
DIODONTIDÆ
TETRODONTIDÆ
OSTRACIIDÆ
BALISTIDÆ
MONACANTHIDÆ
AGONIDÆ
PEGASIDÆ
TRIGLIDÆ
LIPARIDIDÆ
CYCLOPTERIDÆ
COTTIDÆ
PLATYCEPHALIDÆ
GOBIIDÆ
TRICHIURIDÆ
ZEIDÆ
HETEROSOMATA
PLECTOGNATHI
SCARIDÆ
SCORPÆNOIDEI
CERATIIDÆ
ANTENNARIIDÆ
MALTHIDÆ
LOPHIIDÆ
PEDICULATI
HEXAGRAMMIDÆ
SCOMBRIDÆ
CHÆTODIPTERIDÆ
POMACENTRIDÆ
POLYCENTRIDÆ
CICHLIDÆ
LABRIDÆ
LABROIDEI
SCORPÆNIDÆ
BATRACHIDÆ
CLINIDÆ
BLENNIIDÆ
BLENNIOIDEI
OPHIDIIDÆ
ZOARCIDÆ
BROTULIDÆ
GADIDÆ
MACROURIDÆ
ANACANTHINI
CALLIONYMIDÆ
GOBIESOCIDÆ
ZANCLIDÆ
TEUTHIDIDÆ
SQUAMIPINNES
EMBIOTOCIDÆ
SPARIDÆ
MULLIDÆ
HÆMULIDÆ
CHÆTODONTIDÆ
CIRRHITIDÆ
JUGULARES
NOTOTHENIIDÆ
TRACHINIDÆ
URANOSCOPIDÆ
CARANGIDÆ
CORYPHÆNIDÆ
HISTIOPHORIDÆ
NOMEIDÆ
SCOMBROIDEI
PERCIDÆ
POMATOMIDÆ
SCIÆNIDÆ
ACANTHOPTERYGII
PERCOIDEI
SERRANIDÆ
LOBOTIDÆ
CENTRARCHIDÆ
KYPHOSIDÆ
OLIGOPLEURIDÆ
AMIIDÆ
ACIPENSERIDÆ
CHONDROSTEIDÆ
EUGNATHIDÆ
POLYODONTIDÆ
SYNGNATHIDÆ
CENTRISCIDÆ
FISTULARIIDÆ
RACHICENTRIDÆ
ECHENEIDIDÆ
HEMIBRANCHII
GASTEROSTEIDÆ
SYNENTOGNATHI
EXOCŒTIDÆ
HEMIRAMPHIDÆ
BELONIDÆ
SPHYRÆNIDÆ
ATHERINIDÆ
MUGILIDÆ
PERCOPSIDÆ
POLYNEMIDÆ
PERCESOCES
HOLOCENTRIDÆ
BERYCOIDEI
BERYCIDÆ
GYMNOTIDÆ
CHARACIDÆ
PACHYCORMIDÆ
CYPRINIDÆ
SILURIDÆ
LORICARIIDÆ
AMIOIDEI
OSTARIOPHYSI
CHONDROSTEI
CATOPTERIDÆ
PLATYSOMIDÆ
PALÆONISCIDÆ
SEMIONOTIDÆ
HOLOSTEI
MYCTOPHIDÆ
SCOPELIDÆ
DALLIIDÆ
UMBRIDÆ
ESOCIDÆ
HAPLOMI
PŒCILIIDÆ
STERNOPTYCHIDÆ
STOMIATIDÆ
ALEPOCEPHALIDÆ
CLUPEIDÆ
ISOSPONDYLI
OSTEOGLOSSIDÆ
MYODONTIDÆ
NOTOPTERIDÆ
MORMYRIDÆ
GYMNARCHIDÆ
APODES
SACCOPHARYNGIDÆ
MURÆNIDÆ
ANGUILLIDÆ
MACROSEMIIDÆ
PHOLIDOPHORIDÆ
LEPIDOSTEIDÆ
DAPEDIIDÆ
PYCNODONTIDÆ
SALMONIDÆ
ARGENTINIDÆ
ALBULIDÆ
ELOPIDÆ

Figure 3. Phylogenetic tree of teleosts, based on that of W. K. Gregory as used at the American Museum of Natural History, with some modifications pertinent to present purposes. The blackened areas show the occurrence and distribution of species thought by various workers to resemble leaves or other parts of plants.

for the most part, or in being especially obliteratively marked or formed.

It is difficult to dismiss the works of McAtee (1932) and Robson and Richards (1936) as lightly as does Huxley (1942). These authors are critical of the alleged survival value of close resemblances, even though the present data would seem to support the assumption of such a survival value. While many others have criticized the views of McAtee, *e. g.*, Cott (1940) and Dobzhansky (1941), the most outstanding criticisms appear to be those given by Fisher at a meeting of the Entomological Society of London. Of the several speakers at this meeting, Fisher (1933), who gave a caustically critical analysis of McAtee's methodology, presented a most impressive case. Resemblances do exist, but as yet it can be *assumed* only that they are of a commonly ascribed value to the creatures so constituted. Probably an analysis along the lines of that suggested by Pearl (1930) would be necessary to establish or demolish such ideas, but such a program cannot be easily undertaken until someone with time, equipment and finances can support it. In the meantime speculation must continue to occupy much of this field.

If the views of the critics are accepted, and if it is argued that selection is not operative since basic proof is not available, then unfortunately there is no alternative explanation, plausible or otherwise. The preceding discussion has been given with the assumption that there is validity to the idea that some form of natural selection does operate in these matters. Actually, all that can be said is that when such features of resemblance appear they do make for concealment, but that the majority of fishes manage very satisfactorily without them. It is to be noted in this connection that the fishes listed are not conspicuously numerous in either species or individuals as compared with such relatively non-hidden forms as some of the herrings, serranids, cyprinids, scombrids, *etc.* In other words, whatever the biological significance of these resemblances, it has not led to a great world-wide dominance of the forms developing such features. Of course, it is possible to hide behind the statement that such a development of resemblance is of great value to the possessor, but one can estimate the value of the several given features only when the totality of attributes are considered. This is at once sound and peculiarly unsatisfactory. For example, if the number of eggs produced by these different fishes is considered, nothing definite is forthcoming, for while there are no accurate measurements of the numbers in many cases, there is sufficient known about them to be able to approximate each as to egg production with other related species not so modified. On the other hand, the subject might be approached from the standpoint of behavior on another basis—namely that the young of *Chaetodipterus* are not very well streamlined, are unable to swim fast and therefore have to escape their enemies by other means. This is suspiciously like expecting a lift from a tug on one's boot straps. If they were not encumbered with hypertrophied ventrals, *etc.*, they might move a little faster. Young centrarchids for example manage very well although they are just about of the same body depth. Thus an impasse is reached. Since an animal tends to use what equipment it has, presumably by trial and error (both phylogenetically and ontogenetically) and since this results in disaster and elimination if the 'errors' are sufficiently grave, those animals living successfully today apparently have established their particular behavior both because it was useful, or at least not lethal or strongly detrimental, and because their available mechanical means so permitted. Perhaps it should not be surprising that so few fishes closely approach plant structures, or anything else, in detail, and that so many have vague resemblances which, however, effectively hide them, while again fewer seem to depend on countershading alone. After the general level of effective vague obliteration is reached, it is hard to imagine why such modifications have gone further. Some peculiar habit based elsewhere, such as lolling in the surf, might of course conceivably invoke a new level of selection. Such a new level might, for example, be rooted in the very good eye of a heron, for as Sumner (1945) reiterates "the cause must have had eyes." Hare (1945) in reviewing Sumner's article would refer the matter to the realm of psychobiology.

Cott (1940) and Huxley (1942) discuss at great length the resemblances shown by various organisms to animate and inanimate objects. As already indicated, an abundance of illustrations does not *prove* that the condition has been arrived at by any one mechanism, even if only one can be visualized at present as being superficially plausible. Even Conklin (1943, 1944), a stalwart adaptationist, finds it hard to believe that all "adaptations" can be accounted for on a basis of natural selection, and therefore he looks hopefully toward trial and error methods in the reactions as having something to do with adaptation in some undefined obscure manner. In this connection it is interesting to note that flounders, normally with a matching pattern which changes to match the immediate environment, sometimes attain adulthood even though they lack this very marked pigmentation and are a plain and conspicuous white. Breder (1938 b) and Gunter (1943) have recently noted such cases. Except for the closely matching colors and patterns in normal flounders in relation to the bottom on which they rest, and the speed with which they adjust themselves appropriately, these instances probably do not differ functionally from others showing similar lack of pigment. This also would seem to apply to albinism, melanism and various kinds of metachromatism. The considerable literature of these conditions gives some measure of the extent to which such aberrantly colored fishes occur and manage to survive to adulthood.

It might be argued that the cases discussed herein are not strikingly abundant, and that it is just these special developments which have, at some stage in their history, kept them from extinction. This is like saying that under the pressure of a population-reducing predation such variants saved the strain. This would call for a bias in a given direction, for vague resemblances to all manner of objects which could perhaps produce the more common "general resemblances" would be expected. But this is hard to reconcile with the closely drawn cases. What would initially precipitate an evolutionary process for a definite and single type of resemblance in a given species? Hubbs (1941) discusses at length various general resemblances of parallel and diverse kinds in a variety of situations, but unfortunately he does not go into the question of the more exact similarities. Simpson (1944), discussing similar matters, wrote, "Some degree of mimicry is evidently adaptively useful, but do predators really distinguish between approximate resemblance and the very exact resemblance often involved in mimicry?"

Another approach to this problem might be made if one considers these fishes as making the best of a bad bargain. If either gene linkage or pleiotropism is assumed to associate an awkward shape with a greater fecundity, for example, then a rather different point of view may be obtained. In this connection Hubbs (1940) wrote,

> Naively, some have held that the so-called non-adaptive, specific characters may have come into expression because they are genetically associated with an increase in fecundity. How much more objective it would be to lay stress on the selectional advantage of the increased rate of reproduction as the

> essential change, even though it be hidden from view, and to regard the associated morphological change as a secondary consequence, which in itself might have been of neutral or even negative significance.[7]

If it is assumed on this basis that the present close resemblances are merely a residue of many that were not sufficiently successful to allow the individuals to exist, the problem then becomes one of statistics. One may ask, how many such close resemblances have appeared in the entire evolution of fishes? Are these the dying gasps (in an evolutionary sense) of species far off a successful track? In this connection Sumner (1942) said:

> For we may, on the other hand, conceive of natural selection as acting continuously throughout the evolutionary process and accumulating small variations in the direction of fitness; or we may conceive of it merely as setting its stamp of approval upon the finished product. In the latter case, the role of natural selection is greatly restricted, and we must look elsewhere for the origin of adaptations.

The lengthy discussions of Mayr (1942) and Huxley (1942) on the significance of the apparently selective value of characters of many kinds in relation to the genetic constitution are suggestive in this connection. The remarks of Lutz (1924) on certain aspects of insect variation in structure and function certainly bears on any such discussion and should be consulted. Critical study of cases of the present sort should be helpful, but the accumulation of many more facts on the occurrence of these close resemblances, on the behavior of their possessors and on the success of predators in circumventing this type of hiding is badly needed.

A possible means of critical evaluation of the survival value of special resemblance arises in connection with the relation between the range of a given species as compared with the special environments which make possible the obliterative resemblances that have been under discussion. It would appear that only two possibilities are present. 1. The species are limited to the ecological niches that provide the "stage" for making the disappearing act possible. 2. The species are not limited to such environments and the phenomena occur through only part of the range.

Of course, in the first group it is understood that migrations or other wanderings from the environmental setting would be permitted at times when the species are in certain stages of development when they may not show the "resemblance." Although we know of no cases where such phenomena are known to be persistent throughout development, such wanderings off the stage should be expected. In most cases it would be impossible for any fish to show a marked resemblance to a single object throughout its life, since a fish generally changes radically in size and usually in general appearance as well, a necessary concomitant of growth. It is of interest in this connection that in the various species listed in Table I, none shows a resemblance to one item at one stage and to another at a later stage, so far as known. In all cases evidently one such "resemblance" suffices, either when the fish are young or adult. The periods of special resemblance of the Syngnathidae, *Doratonotus,* and *Monocirrhus* may represent a very large part of the life history. In these instances it is the adult which was described as resembling plants, and it is not certain that such resemblances as exist in the young forms could confer any benefit, but it would seem that they might. Young Syngnathidae are generally planktonic, and it is far from certain at just what time they take up residence in a resembling environment and at what size and age they should be classified as in Table I. The young stages of *Doratonotus* are not known, but they probably resemble the adults and thus a smaller bit of green *Ulva.* Quite small *Monocirrhus* in an aquarium closely resemble their parents and act in an essentially similar manner. In a state of nature it is not recorded whether these small sizes are as inconspicuous as the adults. However, it would seem that whatever inconspicuousness they do have would result from a general resemblance to the background, since it is extremely unlikely that leaves of only a few millimeters would have the same form as the young fish or that these leaves would be shed in significant quantities at the appropriate time (p. 8).

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[7] This thought has been brought up frequently in various guises, and, as Sumner (1942) indicates, it is to be found in Darwin's *Origin of Species*.

In the second group of possibilities it is known that at least a number of species occur at the "resembling" sizes in regions which do not permit the appearance of the observed phenomenon. The question which arises here is whether such species are kept from extinction by a constant migration of individuals from areas where this resembling performance is possible (those in other situations being considered as peripheral wastage), or whether those fishes outside the resembled environment are specifically successful, so that the protective value of such resemblance is unnecessary and truly accidental. Obviously these two opposed propositions are the extremes and any intermediate phase might actually obtain.

Admittedly our data are still too meager to carry this thought very far, but if we consider only those forms about which we have some evidence, then it is possible to indicate at least some paths of research that should be fruitful. Considered species by species, we have the following data as a starting point.

The "stick-fish" stage of *Lepisosteus* evidently becomes apparent as a mimic where there is appropriate material and so impresses an observer, whereas in a region where there is no material of a suitable kind a different observer has no thought of such a possibility (p. 3). The form is obviously highly successful in both types of environment. A detailed study of a possible differential adjustment of behavior of *Lepisosteus* in this stage in both the Michigan lakes and the Florida Everglades should be illuminating.

The young "stick-fish" stage of *Tylosurus raphidoma* is very abundant about the Dry Tortugas where there is an abundance of "sticks." On the other hand, *T. raphidoma* is much less abundant on the Florida west coast where such debris is not as common or as similar. The young fishes are reported from many places and it is certain that they wander or drift far from their center of abundance, even as far as New York harbor (Breder, 1938a). How much of this distribution should be considered "peripheral loss" cannot be determined at this time.

The resemblance of one and possibly two species of *Cypselurus* to *Barringtonia* flowers in the Pacific Ocean would seem to be a very special case, since *Cypselurus* is a widespread genus and obviously occurs in places where there are no *Barringtonia.* Thus Caribbean species, very close in appearance to Pacific species, evidently bear a "resemblance" to an item which does not exist in their particular environment.

The family Syngnathidae appears to be rather closely associated with algae and weed to which they bear a greater or lesser degree of resemblance. This particular "resemblance" may be more definitely associated with other factors such as habit and absolute size (see Breder and Edgerton, 1942). It is noteworthy that *Syngnathus fuscus* Storer, which inhabited the *Zostera* of New York harbor before that weed suddenly disappeared some years ago, showed no evident decrease in numbers after its disappearance; they could be taken throughout this period of complete absence of the plant, on clean, sandy bottoms where the weed had formerly grown. While there is no statistical measure of its relative abundance in relation to the presence or absence of the weed, the species still exists in what is apparently normal quantities.

Oligoplites breeds in places where no mangrove or other plant sheds lanceolate leaves in the sea. The ready change of habit and color of this fish (p. 7) raises the question of whether or not these fishes assume the color and stance of dead leaves only in the presence of the latter. More basic evidence on this problem would be of considerable significance in connection with the role of behavior in such matters.

Lobotes shows its so-called "leaf-like behavior" long after it is bigger than any leaf that is commonly found drifting in the sea. In this case the causes of such behavior may be rooted elsewhere in the economy of the species.

Monocirrhus and *Doratonotus* have already been discussed. Perhaps the former is comparable to *Lobotes* in a sense, although it grows into the appropriate size instead of out of it. Regarding *Doratonotus* we have too little data for discussion.

The behavior of young *Chaetodipterus*, as fully set forth herein, changes with confinement; Burkenroad, in a personal communication referred to previously, has described very different behavior in a region not having mangrove trees. Thus this peculiar behavior may be associated only with the presence of mangrove buds. Note especially that these young fish, on the Florida west coast at least, attack each other rather than "school," a behavior which may serve to space them nicely in a scattered field of mangrove buds and snails. *Platax* is insufficiently described to discuss, but may well engage in a behavior similar to that of *Chaetodipterus* or *Oligoplites*.

The young of *Cyclopterus* appear to huddle close to any object; it shows color-matching abilities in the western Atlantic, but on the European side it closely matches a definite object not only as to color but also as to form.

The peculiar attitude of *Alutera* appears to be of deceptive value only at a certain size and in certain places. This behavior may be essentially similar to that of *Lobotes*. It would be interesting to know if the young stand on their heads for longer periods of time or more frequently than the adults in the presence of suitable weed, or if they tend to remain longer in weed than over bare bottom.

Heterostichus could at least spend its entire life amid *Macrocystis*.

It would be worth while to find out if it does and if there is a sorting out of sizes of fish and sizes of thalli.

From the foregoing paragraphs it should be evident that much analytical field work must be undertaken to understand even gross features of special resemblance before much can be gleaned concerning the role of behavior in such matters.

Far too little is known at present about the extent of the geographical range useful to the continued maintenance of most of these fishes to permit an extended analysis of the environment with regard to presences or absences. It may be pointed out that many fishes do change to a color closely matching their immediate or particular environment; such instances have been omitted from the present list. In lower New York harbor in late summer, when small specimens of *Tautogo onitis* (Linnaeus), *Monacanthus hispidus* (Linnaeus) and *Lactophrys trigonus* (Linnaeus) are fairly common, the author has often observed that those seined amid sheets of *Ulva* are of a uniform, closely-matching bright green, a fact which makes sorting them out of a catch a time-consuming task. On the other hand, those taken elsewhere are always colored with various shades and mottlings of browns and greys. Perhaps this might be similar to the conditions found in the corixids. The work of Sumner (1935) on *Gambusia* would seem to be applicable here. *Chaetodipterus* young are found in regions remote from mangroves, and perhaps they behave differently under such conditions. As with *Oligoplites*, this is discussed in another connection (p. 7). We do not know enough about other fishes to warrant any discussion at this time, but the situation clearly points to the desirability of obtaining more extensive information on this aspect of the problem.

The role of behavior in connection with these phenomena is in need of further study also. Clarification of this problem in part awaits more data and analyses of the social attitudes of fishes generally. Since fishes may seek a solitary existence, or exist in aggregations or schools, their behavior in this regard is inextricably involved in their tendencies to seek particular visual patterns. The difference in the type of object sought and approached by young *Tylosurus raphidoma* and *Strongylura notata* has already been noted, and this may be the foundation responsible for the differences in their juvenile behavior patterns. *Cypselurus*, at a size when it resembles *Barringtonia*, is not a closely aggregating form although it is when adult; it presents a different type of resemblance relationship from that of *Tylosurus*.

Tylosurus actually nestles up to an object which resembles itself and which is numerous but scattered. *Cypselurus* does not nestle up to anything, but resembles an object also numerous and scattered and merely present in the same general area.

From this discussion it should be obvious that for any serious analysis of the problems arising from such close resemblances considerable data on at least the following items should be obtained before it would be possible to hazard even a rough estimate of the likelihood of such features being of utility to the species in question.

1. Compare the range and time limits of the special environment in which such deceptive resemblance is possible with the total range and time limits of the species at the ontogenetic stage in which the resemblance occurs.
2. Determine the behavior of the species both in the presence and absence of the pertinent environmental items as to color change and pattern and as to attitudes and motion.
3. Determine the range and actual physical presence of predators as compared with the environment and the total range as outlined under item 1.
4. Determine if the population is based largely on production limited to the areas permitting deceptive resemblances or if there is a significant production out of it.

Since the deceptive nature of these resemblances is admitted and since laboratory experiments have shown that various captive, but more or less normal predators may be deceived [*e. g.*, Sumner (1935), Popham (1942, 1944)], field work somewhat of the nature above outlined is evidently in order. While such a program calls for considerable work it is clear that none of the items is impossible to determine. The thorough study of one or two such cases should go far toward clarifying the entire question.

SUMMARY

1. Seventeen genera of fishes have been described as bearing a close resemblance to various parts of plants. All but two of these are from the marine littoral zone.
2. In all but three orders, acanthopterygians are involved; these developments are clearly independent in each case.
3. Seven genera show resemblances to plant parts as adults, these adults necessarily being permanently small, while another 10 display

them as young, these abandoning the similarities on outgrowing the size of the objects.

4. Eleven genera show resemblances to floating objects, while only six show them to attached growths. Nine genera resemble terrestrial plant parts which regularly fall in the water and eight genera resemble aquatic vegetation.

5. The special resemblance of the young of *Chaetodipterus faber* (Broussonet) of a certain size to the infertile seed pods of the red mangrove, *Rhizophora mangle*, which are found in the sea at the time when these fish are in this deceptive state, is described. The association of young *Chaetodipterus*, the mangrove buds and snails (*Cerithium*), all of about the same size and all dull black as seen against a background of light sand, causes considerable confusion to the human observer.

6. Three cases of non-venomous fishes allegedly mimicking poisonous fishes or sea snakes are cited.

7. The current usage of the word "adaptation," as well as its meaning and significance in connection with matters considered in this present paper, is discussed.

8. The alleged survival value of the special resemblances of fishes to plant parts is considered, and suggestions are made for critical studies of the biological significance of such resemblances.

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A SYSTEMATIC AND ECOLOGICAL STUDY OF THE HALACARIDAE OF EASTERN NORTH AMERICA

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A SYSTEMATIC AND ECOLOGICAL STUDY OF THE HALACARIDAE OF EASTERN NORTH AMERICA[1]

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ABSTRACT

This study is based upon collections of Halacaridae from New Brunswick, Canada, Long Island Sound, Chesapeake Bay, North Carolina and southern Florida. Improved methods for making permanent preparations of mites were developed and are presented in detail.

The morphology of several structures, including the tarsus, ambulacrum, lateral claws, rosette pores and genito-anal area is discussed and their taxonomic significance is pointed out. Keys to all subfamilies, genera and subgenera are given and two genera and one subgenus are newly described. The subfamily Rhombognathinae and the genus *Copidognathus* are revised along natural lines and the nomenclatorial status of several genera and species is clarified. The general and detailed anatomy of the species is illustrated by 330 figures. A glossary of terms is given, and all important structures, including the newly named ones, are labelled in at least one figure.

The number of species, subspecies and varieties from eastern North America is increased from 4 to 41, of which 14 are new. Only two of the four forms known from previous works were rediscovered. Keys to the North American species are given.

The halacarid fauna of Florida is the richest on our eastern coast, that of New England is the second richest, and intermediate regions are the poorest. There is no correlation between the New England-New Brunswick fauna and that of Florida. The fauna of southern Florida is tropical in character and is closely related to that of the Dutch West Indies and Bermuda. Nearly 70 per cent of the forms in the American Boreal Atlantic are identical with, or closely related to, forms in the European Boreal Atlantic. The transitional nature of the fauna between the

American Boreal and Tropical regions is shown to consist more of a dropping out of some Boreal genera than of an overlapping of Boreal and Tropical species. The distribution of certain species or species groups in the Caribbean, Mediterranean and southwest Pacific regions suggests a Tethyian halacarid fauna parallel to that of other groups of animals.

The fauna of the subtidal zone is more uniform than that of the intertidal zone, especially from a qualitative standpoint. Limited collections near the eastern end of Long Island Sound suggest a transition from a eulittoral to a sublittoral fauna. Observations on the absence of certain Rhombognathinae from special nontidal habitats indicate that some species require periodic exposure to air, thus accounting for their absence from the subtidal zone.

A well developed sand fauna consisting of three psammobiont and one psammophile species is found in Long Island Sound. The fauna is very similar to that of Europe. Of the faunae developed upon molluscs, those on *Modiolus* and *Ostrea* are most complex. The encrustation of *Modiolus* by *Balanus* greatly increases the ability of this substrate to support an halacarid fauna.

The algicolous faunae are dominated by the Rhombognathinae; none of the Halacarinae are typically algicolous. Estuarine habitats, because of their low salinity, are characterized by halacarid faunae containing a small number of species.

ACKNOWLEDGMENTS

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R. V. Truitt, director of the Chesapeake Biological Laboratory, and his staff extended every favor to the writer during his stay at Solomon's Island. H. F. Prytherch, Aquatic Biologist in charge of the United States Fishery Biological Laboratory at Beaufort, North Carolina, and his staff were equally generous in providing laboratory facilities and transportation during the time the writer was at Beaufort.

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INTRODUCTION

History of the North American Fauna

The history of our knowledge of the Halacaridae of eastern North America is brief and unimpressive. The first record of the occurrence of members of this family on western Atlantic shores was in 1871, when Packard (1871a) described *Halacarus* (*Thalassarachna*) *basteri* (Johnston) 1836 from Eastport, Maine, under the name of *Thalassarachna verrilli*. Packard did not recognize the affinities of this mite with the few European Halacaridae which had been described and properly named at that time; in fact, he attempted to ally it with the fresh-water mites. Trouessart (1893d: 259–261) described *Copidognathus* (s. str.) *poucheti* from Spitzbergen and stated that it also had been found on calcareous algae (*Lithothamnion*) from Labrador. Kramer (1897a: 83) listed two species from the west coast of Greenland (Sermilik Fjord). One of these he identified as *Rhombognathus notops* (Gosse) 1855, but the other species was represented by a single larva and was listed simply as a species of *Halacarus*. Trägårdh (1905a: 63) misidentified a specimen of *Halacarus* (*Thalassarachna*) *basteri* from Greenland as *Agauopsis hirsuta* (Trouessart). He did not know the precise locality. Gimbel (1919a: 124–128) described *Copidognathus* (s. str.) *punctatissimus* from Newport, North America (presumably Newport, Rhode Island) and this species is redescribed in this work from numerous specimens taken by the writer. Finally, the present writer (Newell, 1945a) has recently shown that *Thalassarachna verrilli* Packard 1871 is none other than the well known *Halacarus basteri* of Europe.

Therefore, up to the present time five species of Halacaridae have been listed from the shores of Greenland and eastern North America, and one of these (*Halacarus* sp. Kramer 1897) is not recognizable because it was not described. The North American species have never been treated from an ecological or zoogeographic standpoint. The purpose of this work is to describe as great a portion as possible of this virtually unknown segment of our marine fauna, to determine in so far as possible what factors affect the ranges and habitats of the various species, and to study the relationship between the fauna of our shores and that of other parts of the Atlantic region. In addition, a number of contributions to the systematics and morphology of the family as a whole have been made in the course of the study, and these are presented in detail.

Equipment and Methods

Collecting and sorting. At each locality as great a variety of substrates as possible was sampled and the material was taken to the laboratory for study. In most cases 500 ml. samples were found to be as large as could be examined in a reasonable length of time. Paraffined "Sealright" containers, used for packing dairy products, were found most convenient because of their lightness. Sand samples were washed in a battery jar with a fine, strong jet of tap water, and the water was decanted quickly into a second jar. The washing was repeated until the sand was thoroughly cleaned. Large materials such as algae, molluscs, sponges, *etc.*, were placed in a sieve with 2 mm. apertures while being washed. The washings were freed of all silt and other fine material by washing over a sieve with apertures of 0.1 mm. The residue was then washed through a series of sieves with apertures of 1.0, 0.5, 0.25, and 0.1 mm., except in the case of samples with a small amount of detritus in the 0.5–0.1 mm. fraction, where the 0.25 mm. sieve was omitted. The time required in washing the residue through this series of sieves was more than regained in sorting the mites from the residue, for the specimens could be seen easily and removed quickly as they crawled about on particles of their own size. If too much water accumulated in the various containers during the process of sieving, the jars were set aside for three or four minutes and then decanted through the 0.1 mm. sieve to catch any specimens which might adhere to the surface of the water. The fractions were placed in 100 ml. beakers, after which concentrated (4 times) sea water was added to give an approximately natural solution.

The residue was examined under the binoculars in convenient quantities in a square dish with a ridged bottom. Specimens were transferred to a small dish by means of a fine pipette. In population studies, the more easily recognized species or stages were simply recorded and not removed unless wanted for special purposes. The others were removed and subsequently placed on a ruled slide, crushed under a heavy cover slip and counted under the compound microscope. Any forms intended for preservation were removed from the slide and mounted as described below.

Preparation of mites prior to killing. As a rule the mites collected from marine habitats have a variable amount of detritus clinging to them. The simplest way to eliminate this is to place the live mites in a small dish of clean sea water with a very thin layer (3–4 grains deep) of clean white sand of uniform texture (*i. e.*, with all of the coarser and finer fractions sieved out). After a few hours of crawling about, most of the mites become quite clean and exceptionally dirty specimens can be transferred to a second sand dish. When clean the mites are transferred to tap water in deep depression slides (capacity ca. 1 ml.), at which time the species or stages are segregated. Mites which are obtained from samples which have been washed through sieves in the manner described previously usually require no further cleaning.

Killing. With a sharp needle the mites are pierced ventrally, and with a second (dull) needle the greater part of the gut contents is forced out, this latter procedure being absolutely essential in the case of the more heavily pigmented forms (Rhombognathinae). The specimens are then syringed to free them of as much as possible of the extruded material. This leaves the weakly armored mites somewhat crushed, but these regain their form in the process of digestion in trypsin. An alternate method of evisceration is as follows. The mites are placed in a small drop of water on a clean slide, a cover slip is then dropped on them and pressure is applied with a fine needle. The cover slip is removed, the mites are washed into a depression slide and transferred to the trypsin tubes. This method is especially convenient in faunistic studies, for identification can be made on the slide and specimens which are not needed for preservation can be discarded. However, the large species often remain flattened by such treatment, thus being permanently distorted. These are best treated by making a fairly deep incision in the side of the mite with the broken corner of a razor blade and gently forcing out most of the gut contents. By this method less compression is required to clean the specimens and distortion is less frequent than when the specimens are pierced or crushed.

Preparation of digestion tubes. Convenient trypsin tubes can be prepared as follows. A vial with an inside diameter of 12 mm. is scored with the sharpened end of a three-cornered file 2 cm. from the bottom of the vial. The vial is rotated in the corner of the lid of a microscope slide box, with the sharpened corner of the file held against it. The vial is then rotated in a microflame (3 mm. long) with the flame touching the scratch on the vial, thus producing a very smooth cut. The upper edge is levelled by rubbing it on a wet carborundum. Covers are made from vials just large enough to slip over the 12 mm. vial, these being cut in the same manner as outlined above but only 10 mm. long. Small vials with an inside diameter of 4–5 mm. are then cut 15 mm. long. The trypsin digestion solution is placed in the small inner vial, the toluene in the outer one.

Digestion. Halacaridae cannot be treated with even dilute solutions of alkali, as these dissolve the outer layer of the cuticle, thus rendering the plates practically invisible and destroying the characteristic sculpturing on them. The digestion solution is prepared by dissolving 0.2 g. of powdered trypsin in 10.0 ml. of 0.5 per cent Na_2CO_3 and filtering after the solution has been allowed to stand several hours, during which time it must be protected by storage in an atmosphere saturated with toluene. It should be filtered at least twice with the same filter paper. This solution can be stored in a refrigerator, but the writer has obtained the best results by using a screw-cap storage bottle patterned after the digestion tubes, that is, with an inner well having a capacity of 10 ml., surrounded by cotton or paper towel (to reduce the likelihood of spilling) saturated with toluene. Trypsin has been kept as long as a month in this way, whereas refrigerated trypsin without toluene cannot be kept clear for more than a few days. Mites are left in this solution 24–72 hours in a humidor at 40° C. After the body contents have been adequately digested the specimens are washed in distilled water and transferred to the dehydration dishes.

Dehydration. Small stender dishes (30 mm. inside) are fitted with a square piece of microscope slide which is cut small enough to lie in contact with the bottom of the dish. The mites are transferred to a drop of water on this plate and the legs are pulled into proper position by using a very fine needle and by taking advantage of surface tension to hold the specimens. A small circular cover slip is carefully dropped onto the flat drop of water containing the specimens. Excess water which may hold the slip far above the mites is removed so that the mites are held quite firmly but without crushing. Absolute alcohol is pipetted onto the cover slip until the dish is filled to a level just above the cover slip. The alcohol gradually diffuses under the cover slip and dehydration is completed within an hour or so.

Infiltration with alpha-chloronaphthalene (*acn*). The specimens are transferred from alcohol to small tubes with an inside diameter of about 4 mm. If it is suspected that an appreciable quantity of water is still present it is necessary to add fresh absolute alcohol. All but the bottom 2 mm. or so are pipetted off after a half hour, and acn is carefully added by flowing it down the side of the tube rather than by dropping it directly into the alcohol. The acn sinks to the bottom, thus forcing the alcohol and mites to rise above it. Because of the small diameter of the tube, infiltration is slow and distortion is avoided. The alcohol is driven off in an oven at 40° C.

Mounting in Hyrax. When evaporation of the alcohol is complete, the mites are transferred by means of a flattened, bent dissecting needle, first to clean acn and then to "Hyrax" dissolved in acn. Round cover slips 10 mm. in diameter are fastened to a glass slide by means of a very small quantity of glycerine (*not mineral oil*, which causes Hyrax to become heavily clouded). A thick film of the Hyrax-acn mixture is spread over the cover slips, the mites are transferred from acn directly to this film, and these preparations are then placed in an oven at 40–50° C. for three or four days. Because of the low volatility of acn, infiltration with Hyrax is slow and distortion is reduced to a minimum. The dry Hyrax preparations (which should be hard when cooled to room temperature) are inverted on clean slides and gently warmed on the bottom of the warming oven. Pressure is applied with a small lead weight placed on the cover slip.

Specimens of even such weakly armored forms as *Metarhombognathus armatus americanus*, n. subsp., showed less than five per cent decrease in length when mounted by the above method. A series of 12 specimens of *Copidognathus arenarius* n. sp., averaged 315.1μ before dehydration and 317.2μ in the finished mounts. The discrepancy is well within the limits of error, since the measurements were made at low magnification. Eleven specimens of *C. punctatissimus* averaged 314.4μ before dehydration and 308.2μ after the mounts were completed, showing an average reduction of only 2.2 per cent in length. Such forms mounted in balsam, *etc.*, by the usual methods would shrink about 10 per cent. But the principal benefit from this method is the high degree of optical contrast obtained. When completely dry, Hyrax has a refractive index of 1.72 or more, and since that of the cuticle of the mites varies around 1.5, even the most minute cuticular structures are usually clearly defined. Berlese fluid, glycerine jelly, balsam and other standard mountants are entirely unsatisfactory for Halacaridae; and the first two, because of their lack of permanence, should never be used for more than cursory examination of any mite.

Although the technique outlined above was not completely developed until about 1943, the writer has specimens which were mounted in Hyrax in July of 1940 by less satisfactory methods. Six years later the only noticeable change is a slight darkening around the edges of the mounts, and this is not as great as in balsam mounts prepared at the same time. Hyrax is evidently as stable as balsam, and its optical properties make it incomparably superior to the latter as a mounting medium. Mites of many groups can be satisfactorily mounted in Hyrax by the above method. These include most Parasitoidea, small Trombidoidea, Acaroidea, all but the darkest Oribatoidea and isolated skeletal portions of all groups. In a few cases the soft parts can be safely hydrolyzed in five per cent KOH at room temperature, but wherever possible trypsin should be used, for specimens treated with alkali are usually brittle when dehydrated and the setae are especially liable to be broken off due to a general weakening of the cuticle.

Mounting in Clarite. Large and deeply pigmented mites can often be mounted in Clarite, with or without previous hydrolysis of the soft parts. They are killed by pouring hot (60–80° C.) 90 per cent insect saline or 60 per cent alcohol over them. These solutions are slightly hypotonic and the osmotic pressure built up inside the specimens extends the legs, but hot water alone should not be used as this is too hypotonic and usually causes distortion or rupture of the specimens. The mites are dehydrated in small vials or in dehydrating dishes by the same procedures outlined above, but methyl salicylate is substituted for acn in the next step. It is pipetted very carefully down the side of the tube as was the acn and the mites and alcohol lie above it. The alcohol is driven off at 40° C. and the mites are then mounted directly in Clarite. Because dry Clarite is so brittle it is advisable to mix 77 parts of dry Clarite with 23 parts of mineral oil (by weight) before dissolving it in toluene[3]. If the specimens show a tendency to become evacuated (*i. e.*, to become opaque because of the removal of methyl salicylate before infiltration with Clarite can take place) it may be necessary to pierce the specimens to allow more rapid entry of the mountant. Evacuation occurs commonly when mites are transferred from toluene or xylene to resinous media, but only rarely if the less volatile methyl salicylate is used. Valuable specimens in which this occurs can be recovered by running back to methyl salicylate (or to alcohol if too brittle), piercing and remounting. Careful comparative tests show that mineral oil is less satisfactory than methyl salicylate as an infiltrating medium prior to mounting in Clarite because it causes greater distortion.

Permanent glycerine mounts. During the course of this study the writer has developed a method for making glycerine mounts which show promise of being relatively permanent, at least as permanent as Berlese fluid or glycerine jelly preparations and with far better optical properties. Furthermore, it is more adaptable, since the most delicate organisms can be infiltrated with glycerine with little or no serious distortion, whereas gum or gelatinous media are often useless for these. The technique may appear involved and tedious at first glance, but large numbers of slides can be produced with a small output of time per slide when the materials are assembled and the routine is properly organized. Essentially the technique involves mounting the objects between a small and large cover slip, flooding the preparation with a thermoplastic sealing compound, drying, and attaching the cover slip preparation to a slide with the aid of heat. The procedure is outlined in the accompanying diagram, in which the letters correspond with the letters in the following descriptive account.

For convenience in handling the cover slip preparations during the initial steps a special slide is used which consists of a 3 x 1 inch glass slide to which two half inch squares of glass are cemented by means of Clarite (Text-Fig. 1 A). These slides can be used indefinitely, of course, and need be prepared only once. A very small drop of glycerine is placed on the glass square (B), and a clean 22 mm. cover slip is placed on it (C), where it is held firmly by the glycerine. A drop of *anhydrous* glycerine is then placed on the upper surface of the cover

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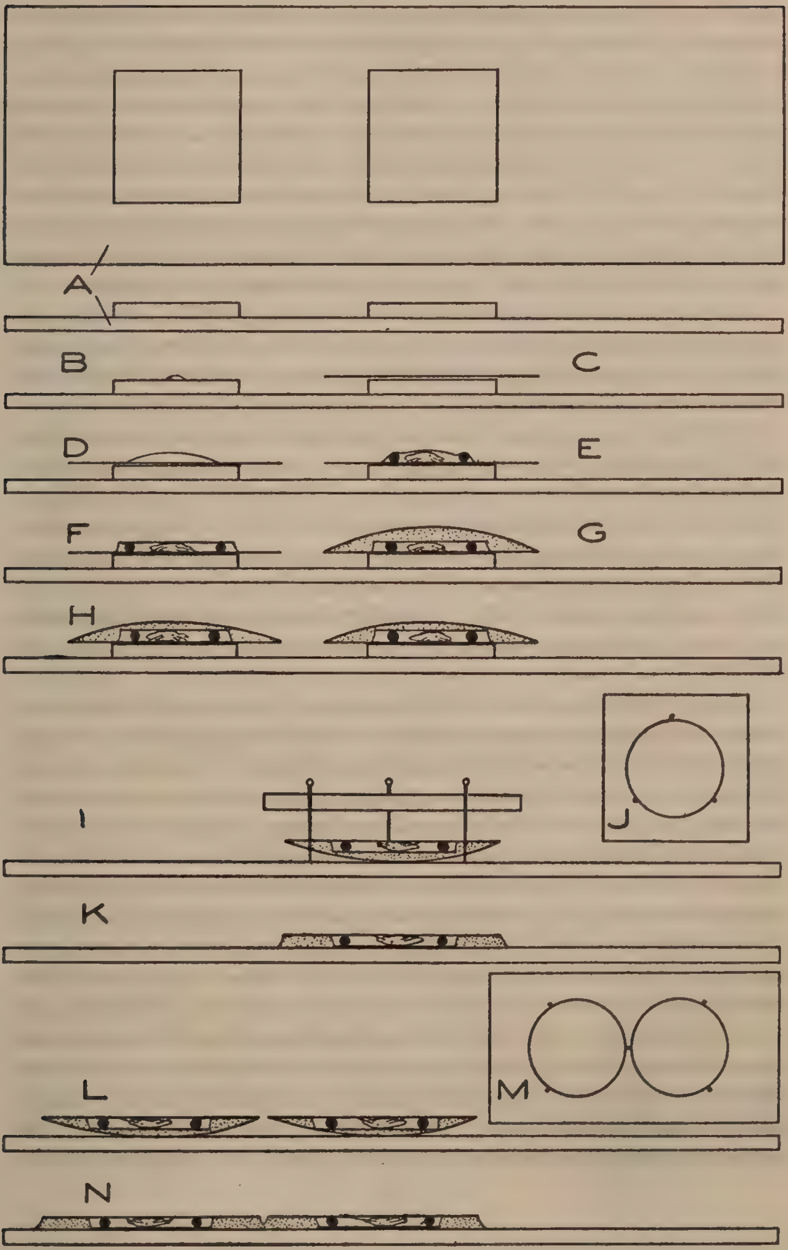
[3] The use of mineral oil to reduce the brittleness of Clarite was suggested to the writer by Alexander Petrunkevitch. Further details on the preparation of Clarite-mineral oil mixtures are given on page 12.


A
B
C
D
E
F
G
H
I
J
K
L
M
N

Text-Figure 1

slip (D), the amount depending upon the size of the objects to be mounted. The specimens are transferred to the glycerine (E), along with glass supports if these are necessary (shown as glass rods in cross-section in the text-figure). A 12 mm. cover slip is placed over the glycerine containing the specimens (F), and the preparation is flooded with a solution of Clarite and mineral oil dissolved in toluene (G). Complete details for making the Clarite mixture are given at the completion of this account. Some experience will be necessary to judge the quantity of sealing mixture required to produce the best mount, but complete failure even on the first slides would be difficult.

The preparation is now placed in an oven set at 40° C. for one or two days, and finally it is left on the bottom of the oven near the heating element for another day, or until the sealing mixture is hard when cooled to room temperature (H). The cover slip preparations are removed from the temporary carriers, inverted, and placed upon a clean slide, either singly or doubly (I, L). The slide is then placed upon a sand bath or hot plate at a temperature of 170–175° C. until the Clarite spreads beyond the edge of the cover slip (K, N). The preparation is likely to slip off the edge of the slide during this step, but this can be avoided by using a tripod consisting of three fine pins or needles set in a thin piece of wood (J, I). A similar device containing five pins is used when two preparations are to be mounted on the same slide (L, M).

Clarite 77%, mineral oil 23% by weight, thinned with toluene to a workable consistency, is the formula of the sealing mixture used by the writer, with the materials available to him. The proportions of Clarite and mineral oil are not matters of personal choice, but must be exact in order to obtain a sealing mixture of proper consistency. On the one hand, a very slight excess (0.5%) of mineral oil will result in a mixture that will allow slow movement of the cover slips, especially in warm weather. On the other hand, as much mineral oil as permissible should be added in order to reduce the brittleness of the Clarite and improve its otherwise poor adherence. Since significant differences may be found in different lots of Clarite and especially of mineral oil, it is desirable to set aside a considerable quantity of each for just this purpose and to make up four or five small trial solutions containing different proportions (*e. g.*, 20: 80, 22: 78, 24: 76, 26: 74, by weight), using an analytical balance. These mixtures are dissolved completely in toluene and drops of each solution are placed on a slide and allowed to dry for at least a day on the bottom of an oven set at 40° C. Those mixtures which are too soft or too brittle can be detected readily by pushing a dissecting needle through the dried samples. A second series of test solutions in the critical range may be advisable before selecting the most satisfactory formula. Further tests are unnecessary unless a new lot of either mineral oil or Clarite is used.

It is essential that anhydrous glycerine be used. In wet climates or during wet seasons of the year, special precautions are necessary to keep the glycerine free of water, which may be done by storing it in the warming oven near the heating unit. In damp weather initial steps of the mounting should be completed as quickly as possible, for glycerine is markedly hygroscopic. Under such circumstances it is advisable to place the preparations in the drying oven for two or three hours prior to adding the small cover slip and flooding with Clarite, that is, between steps E and F.

This technique has been found useful for dissected parts of Halacaridae, and also for certain small mites such as tarsonemids, hypopi and many of the small Trombidoidea which are difficult to handle by other means. It is also very satisfactory for Nematoda, Tardigrada, many small insects and Crustacea. However, whole animals must be gradually infiltrated with glycerine if distortion is to be avoided. The specimens are transferred alive or dead to a small dish containing a solution of 28 parts of water, 68 parts of 95% alcohol, 3 parts of glycerine and 1 part of glacial acetic acid (omit acid if $CaCO_3$ is present), by volume. The solution is then allowed to concentrate slowly by evaporation over a period of from one to several days, depending upon the resistance of the animals to deformation. The specimens are mounted in fresh glycerine as outlined above. Some animals, when placed in the infiltration solution, become temporarily shrunken, but eventually they regain their normal form.

Trypsin treatment of mites or other arthropods prior to dissection or mounting is advisable. If appreciable quantities of colloidal substances or oils are present following digestion these should be precipitated or dissolved in absolute alcohol to prevent their detracting from the serviceability of the mount. The writer regards dissections of legs, mouthparts and special structures as indispensable to a thorough study of mites, for even in a large series of specimens of a species not all parts can be examined satisfactorily on whole mounts. Tarsal structure cannot be determined in a satisfactory manner from dorsal or ventral sides alone, and the best way to assure serviceable preparations is to make at least one dissection, but preferably three or four, of each species. By the above method these can be made an invaluable and permanent part of the collection, not merely temporary mounts which must be discarded eventually because of the lack of a satisfactory method of preserving them. Because the mouthparts are so much smaller than the rest of the mite, these are mounted on a separate cover slip, and both preparations are then attached to the same slide (L, M). The legs are usually removed from both sides of the body, and all are oriented in the same manner (*e. g.*, claws to the right, extensor surface uppermost) so that both lateral and medial aspects of each pair of legs are presented.

NOTES ON FIGURES, DESCRIPTIONS AND CONVENTIONS

In preparing the following descriptions and figures as many specimens as feasible have been examined, and the descriptions are believed to approximate closely the true conditions. The most obvious variations have been noted in the text. However, the writer has attempted to make an exhaustive survey of the external anatomy of each species in the belief that close attention to such details as number, form and arrangement of setae on the body and appendages may eventually provide morphological criteria for the recognition of natural groups within subfamilies or genera. With so many details being checked closely it has been impossible to explore the limits of variability in any of them. As a further consequence of this it is probable that some minute details were actually obtained from atypical specimens; but such cases, if present, are extremely rare. As a rule at least two specimens were examined (from different localities if possible); if exact correspondence was noted no further study was made, but additional specimens were studied if differences were found, and the possibilities of local variation and unilateral variation upon individuals were explored.

The tables showing the arrangement of the setae on the legs should be used with the consideration that it is not possible, in practice, to divide a leg segment into perfect dorsal, ventral, lateral and medial sectors; also, setae which are dorso-lateral in position may be grouped with the dorsal or the lateral setae (*etc.*), according to the material examined. Furthermore, it is sometimes convenient to give the number of setae which constitute a characteristic group of setae under a single column, despite the fact that one of their number may have gone somewhat astray (*e. g.*, in the case of the triangle setae on segments three and five of the legs). However, the total number of setae is that which the writer believed to be typical for that segment. Also the bacillum, prebacillum and parambulacral setae *are not included in the tables* but are discussed separately in the text accompanying the tables. The tables showing dimensions of the segments must be used with reasonable caution, for although the figures presented are accurate for the specimen measured, variations certainly occur from specimen to specimen. With the typical adult halacarid having 24 leg segments on each side, it is obviously impossible to analyze the variations found in each. Ratios are always more reliable than absolute lengths. With the ocular micrometer used, and at the magnifications employed, a single micrometer unit had the following values: 6.93μ at 100, 1.66μ at 430, and 0.75μ at 970. Measurements were made to the nearest half unit, so that the measurements are accurate to about 1.7, 0.4 or 0.2μ at the magnifications employed. Most of the species are small enough so that leg segments could be measured under oil immersion, thus reducing the error to ± 0.2μ. Errors due to limitations of the optical equipment would therefore be insignificant, with one or two possible exceptions.

The original drawings were made with a camera lucida at linear magnifications ranging from 160 to 2200, and occasionally at 4000. Scales are provided with most figures and these can be used with considerable confidence to obtain measurements not given in the text, except in certain cases in which structures are drawn in oblique view. These are usually quite obvious, either from the drawings themselves, from notations in the text or from the legends. Not all the drawings for even one of the sexes of any species are from the same individual, of course, except in cases in which a single specimen was available.

The lengths of the leg segments are given in micra, the measurements being the maximum dorsal length measured in a straight line from the base to the end of the segment. Overlapping of segments is usually insignificant. The height of a segment is its maximum height perpendicular to the longitudinal axis of the segment. The length of the tarsus is the measurement to the base of the carpite in the Rhombognathinae, and to the base of the median claw in the other groups, since this point was more easily seen than the true disti-dorsal end of the tarsus. The length of the ambulacrum, then, is the maximum straight line distance from the base of the carpite, or the median claw, to the outermost surface of the claw.

The loosely used terms "swollen" and "not swollen" as applied to leg segments in the Halacaridae are augmented by actual ratios. Those segments with a ratio of length to height (L/H) of 2.0 or more are "not swollen"; those in which L/H is less than 2.0 are "slightly swollen," "swollen," *etc.* This system does not eliminate border-line cases, but it should reduce the amount of overlapping which results from purely descriptive terms.

Where scales have been provided for the drawings, each division on the scale equals 10μ. A scale with only one division represents 10μ, a scale with three divisions represents 30μ, *etc.* In the scales which are 10 divisions long, a slightly longer mark has been made at the 50μ point. There are no exceptions.

The following abbreviations of frequently recurring terms have been employed:

AD	antero-dorsal plate.
AE	anterior epimeral plate.
AD-PD	distance between antero-dorsal plate and postero-dorsal plate.
Ambul.	ambulacrum.
av.	average.
ca.	*circa.*
d.	dorsal (in tables on chaetotaxy of legs).
GA	genito-anal plate.
l.	lateral (in tables of chaetotaxy of legs).
L/H	the ratio of length to height (of a segment).
L/W	the ratio of length to width (of the body, or a plate, *etc.*).
m.	medial (in tables of chaetotaxy of legs).
OC	ocular plates.
OC-OC	the distance between the most medial points on the right and left ocular plates.
P-1	palpal segment one.
P-3	palpal segment three.
PD	postero-dorsal plate.
PE	posterior epimeral plate (or plates).
T/BL	total length of leg divided by the body length.
v.	ventral (in tables of chaetotaxy of legs).

I-6	leg I, segment 6; or, tarsus I.
II-1	leg II, segment 1; or, trochanter II.
III-3	leg III, segment 3; or, femur III.
IV-4	leg IV, segment 4; or, patella IV.

GENERAL SYSTEMATICS

Diagnosis of the Family Halacaridae Murray 1876

Trombidoidea with body typically flattened or, more rarely, circular in cross-section; elliptical in outline. Mouthparts forming a distinct capitulum nearly always projecting well beyond anterior margin of body, but in a few forms completely hidden in dorsal view. Palpi with 3 or 4 segments, attached laterally, dorso-laterally or dorsally to base of capitulum. Maxillary portions of palpi completely fused. Chelicerae retractile, lying in a dorsal groove in rostrum; ventral digit large, movable; dorsal digit reduced to a pointed membrane. Tracheal system very rudimentary and quite certainly not functional in respiration. Cuticle of body wall usually reinforced with 4 plates dorsally (predorsal, postdorsal, and right and left ocular plates) and 4 plates ventrally and laterally (anterior epimeral, right and left posterior epimeral, genito-anal plates), these plates showing varying degrees of subdivision or fusion in different genera, in different species of a single genus, or rarely in the two sexes of a single species. Legs attached laterally, pairs I and II borne on anterior epimeral plate (or plates) and projecting anteriorly; pairs III and IV borne on right and left posterior epimeral plates and projecting posteriorly. Legs with 6 segments in adult. Larvae with only 3 pairs of 5-segmented legs, protonymph with leg IV 5-segmented also, but legs I, II and III 6-segmented. Deutonymph with all legs 6-segmented. Tarsus always with 2 lateral claws; median claw present or absent. Salivary glands well developed. Midgut not opening by way of anus. Anus present, but functioning entirely as an opening for the single, dorso-median excretory tubule. Sexes separate; sexual dimorphism marked in genito-anal plate and genitalia; other structures usually (but not always) identical in form in both sexes. Three eye spots apparently always present; corneae 2, 4 or 6 in number, or absent. Median eye without cornea.

Principally marine, but with numerous fresh-water forms ("Porohalacaridae" of Viets). Not capable of swimming. Predominantly predaceous or herbivorous, but three parasitic genera are known.

Remarks. The assumption that the posterior opening in the Halacaridae is not the anus is not adhered to by the present writer. The fact that there is no connection between this opening and the midgut is unimportant from a morphological standpoint. Unless it be shown (and it would be impossible to do so) that the opening is morphologically and phylogenetically a separate opening from the anus, it is proper and preferable that this opening be called the anus. At the same time its excretory function must not be overlooked. This is in keeping with the principle that homologous structures may, with propriety, be designated by the same name, despite differing physiological adaptations.

The coxae are incorporated into the body wall, forming the epimeral plates. Since the epimeral plates are composite sclerites, which in most forms consist of the modified coxae, plus additional sclerotized portions of the body wall, the term epimeral plate is to be preferred to the terms coxa or coxal plate. The free segments of the legs are, then: (1) trochanter, (2) basifemur, (3) femur, (4) patella, (5) tibia, (6) tarsus. In the larvae, and in leg IV of protonymphs, the basifemur and the femur are undivided and the legs are then composed of five free segments.

KEY TO THE SUBFAMILIES OF HALACARIDAE

1a. Middle piece of claw articulating with carpite, which in turn articulates with (Figs. 25, 48), or is fused with (Fig. 68), end of tarsus. Palpi always very small, sometimes 3-segmented and always closely appressed to sides of rostrum. Gut caeca always green or greenish black. Predominantly marine and intertidal (rarely found in fresh water?) and never living under conditions which preclude algal growth.

  2a. Palpi 3- or 4-segmented, attached laterally. All dorsal plates present and occasionally fused to form a single dorsal plate, in which case corneae are present. Female genital opening terminal or ventral. Principally intertidal (rarely in fresh water?)..RHOMBOGNATHINAE Viets 1927; p. 20.
  Cosmopolitan.

  2b. Palpi 4-segmented, attached dorso-laterally. AD and PD present, OC and corneae absent. Female genital opening terminal, closed by a pair of cusp-like opercula as in genus *Rhombognathides*. Intertidal; arenicolous.
  ACTACARINAE Viets 1939; p. 21.
  North Sea.

1b. Middle piece of claw articulating directly with end of tarsus; carpite absent (Figs. 212, 311). Palpi usually distinctly 4-segmented but usually not closely appressed to sides of rostrum; however, in the few parasitic forms the palpi may be greatly reduced. Predaceous or parasitic (a few may be scavengers) on marine or fresh-water animals. Gut caeca nearly always gray, brown, red, orange, yellow or lavender. Fresh water or marine; intertidal to abyssal.

3a. Palpi attached to capitulum dorsally, separated by an interval no greater than width of base of P-1 (Fig. 329); bases of palpi not clearly visible in ventral view.

4a. Rostrum about as long as palpi (in uncompressed specimens), relatively uniform in width or even expanded distally; opposed to downwardly turned elongate palpi. Rostrum at least three times as long as high. Marine or fresh water........LOHMANNELLINAE Viets 1927; p. 23.
Probably cosmopolitan.

4b. Rostrum much shorter than palpi, less than twice as long as high.

5a. Palpi 4-segmented. Fresh water.
LIMNOHALACARINAE Viets 1927; p. 24.
Europe, Africa, North and South America.

5b. Palpi 3-segmented. Marine.
SIMOGNATHINAE Viets 1927, in part; p. 23.
Adriatic, North Sea, Ireland, Caribbean, Pacific-Antarctic Ocean.

3b. Palpi attached to capitulum laterally; bases of palpi separated by an interval considerably greater than width of P-1, and clearly visible in ventral view (Fig. 313).

6a. Palpi extremely small, 3-segmented.

7a. Parasitic in gut of echinoderms, at least in larval and nymphal instars.[4]
ENTEROHALACARINAE Viets 1938; p. 25.
Western Pacific Ocean.

7b. Predaceous.[4]..........SIMOGNATHINAE Viets 1927, in part; p. 23.
Bay of Biscay; western Indian Ocean.

6b. Palpi 4-segmented, although P-3 and P-4 may be very small or fused; in the latter case the demarcation between P-3 and P-4 is still evident.

8a. P-3 and P-4 greatly reduced, their combined length less than ⅓ that of P-2. Parasitic.

9a. Rostrum and palpi as long as, or longer than, base of capitulum. Rostrum barbed distally, the barbs pointing posteriorly. Ventral digit of chelicerae with coarse teeth. Parasitic, at least as nymphs, on gills of Amphineura.......HALIXODINAE Viets 1927; p. 24.
New Zealand.

9b. Rostrum and palpi much shorter than base of capitulum. Rostrum not barbed distally. Ventral digit of chelicerae with coarse teeth. Parasitic, at least as nymphs, on gills of fresh-water decapod Crustacea.
ASTACOPSIPHAGINAE Viets 1931; p. 25.
Australia.

8b. Combined length of P-3 and P-4 greater than ⅓ the length of P-2. Predaceous.

10a. Genital suckers internal; external genital suckers absent. Principally marine; rarely fresh water.....HALACARINAE Viets 1927; p. 21.
Cosmopolitan.

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[4] Although these characters are undesirable from a morphological standpoint, there are no reliable ones available upon which to base a separation here, owing to inadequate and probably inaccurate descriptions.

10b. External genital suckers present, or with both external and internal suckers. Fresh or brackish water
POROHALACARINAE Viets 1933; p. 22.
Probably cosmopolitan, except in Arctic and Antarctic seas.

KEYS TO THE GENERA AND SUBGENERA

Subfamily Rhombognathinae Viets 1927

1a. Genital opening of female terminal, guarded by a pair of large, cusp-like opercula (Fig. 13). Armor usually heavy. Claws smooth or pectinate; 2 claws on all tarsi, or 3 claws on all tarsi, or 3 claws on I and II and 2 on III and IV. Tarsi I and II with only the bacillum, which is more than five times as long as thick and usually 10 to 15 times as long as thick. Carpite not fused to end of tarsus (Fig. 25). End of tarsi I and II with ventral seta (Fig. 23). Nymphs with genital and anal plates fused............ *Rhombognathides* Viets 1927; p. 47.
French Mediterranean coast, and Connecticut coast of North America northward. Tierra del Fuego, Pacific-Antarctic Ocean (Macquarie Islands); apparently not tropical.

1b. Genital opening of female not terminal, nor guarded by a pair of large cusp-like opercula, but situated in ventral body wall and guarded by a pair of elongate, band-like sclerites at the most (Figs. 5, 55). Either 2 or 3 claws on all tarsi. Tarsus I with bacillum and prebacillum or with only the bacillum (in which case the latter is less than five times as long as thick). Carpite either fused to end of tarsus or free. End of tarsi I and II with or without ventral seta. Nymphs with genital and anal plates fused or separate.

2a. Three claws (in all forms known at present) on all tarsi, with the median claw nearly as heavy as lateral claws. Deutonymphs more heavily armored than adults. Both bacillum and prebacillum on I-6 short, no more than five times as long as thick (Fig. 47). Carpite free. End of tarsi I and II with ventral seta (usually difficult to see). Nymphs with genital and anal plates fused............................ *Metarhombognathus*, new genus; p. 60.
North Sea, and North Carolina coast of North America northward into Arctic Ocean; apparently not tropical.

2b. Two claws (in all forms known at present) on all tarsi. Adults more heavily armored than nymphs, frequently with all dorsal or all ventral plates fused. Only the bacillum present, or with a very rudimentary bacillum and a long, slender prebacillum. Carpite apparently free or visibly fused to tarsus. End of tarsi I and II without ventral seta. Nymphs with genital and anal plates separate.

3a. Tarsi I and II each with a single, short, club-like seta (the bacillum) in front of lateral disti-dorsal seta (Fig. 71). Coxal plates II on right and left sides absent, or, if present, not fused (Fig. 80). Ventral armor re-

duced and not forming a solid plate. Femur I less than 1.5 times as long as high (greatly swollen). Carpite fused to end of tarsus and with a moniliform, flexible shaft (Fig. 64)........*Isobactrus*, new genus; p. 68.
European and American Boreal; Kerguelen.

3b. Tarsi I and II with a stub-like bacillum and a long, slender prebacillum (Fig. 9). Coxal plates II on right and left sides fused (Fig. 3). Ventral armor usually extensive in adult, often forming a solid plate which almost completely encloses genital opening. Femur I usually more than 1.5 times as long as high. Carpite not fused to end of tarsus and with a straight, nonflexible, nonmoniliform shaft (Fig. 1).
Rhombognathus Trouessart 1888; p. 39.
Cosmopolitan.

Subfamily Actacarinae Viets 1939

Represented by a single genus. See characters in key, p. 18. Arenicolous.
Actacarus Schulz 1936.
North Sea.

Subfamily Halacarinae Viets 1927

1a. Palpi apparently 3-segmented, with segments 2 and 3 (or 3 and 4?) fused. Littoral to abyssal..............................*Coloboceras* Trouessart 1889.
French Atlantic coast.

1b. Palpi distinctly 4-segmented (Figs. 110, 202, 319).

2a. P-2 with a medial spiniform seta. P-3 without such a seta. Attenuate distal portion of P-4 shorter than the cylindrical basal portion. Littoral.
Pontacarus Lohmann 1901.
Brazil.

2b. P-2 without a medial spiniform seta, although one may be present on P-3. Attenuate distal portion of P-4 longer than the cylindrical basal portion.

3a. Palpi nearly always relatively straight (Fig. 89). (A line drawn along the ventral surface of P-2 in an undistorted[5] palp forms an angle of less than 30° [usually less than 20°] with a line drawn from the tip of P-4 to the bottom of P-3. Exception: *H. anomalus* Trouessart, easily distinguished by cylindrical body and the division of PD into right and left halves [Figs. 131–137]. This species goes to group 3b.) Rostrum usually parallel-sided, or very nearly so. P-3 plus P-4 shorter than P-2 in probably all species.

4a. Rostrum usually tapering at least very slightly throughout its length and never broader distally than near the base. Capitulum relatively short, never reaching to end of I-3. P-3 often with heavy medial seta. Body and legs never with elaborate lamellae. Leg I often with heavy, rod-shaped setae medially and ventrally......*Agauopsis* Viets 1927; p. 184.
Cosmopolitan.

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[5] Generally, palpi which have been removed from specimens treated with trypsin, or from specimens preserved in 50–60% alcohol (no higher), or in Viets' glycerine-acetic acid-water mixture, will have palpi which are in a natural state of extension, provided there is no distortion from the cover slip.

4b. Rostrum usually distinctly parallel-sided and often slightly broader near the distal end than near the middle. Capitulum often reaching to, or very nearly to, end of I-3. P-3 never with a thick medial seta. Leg I without heavy, rod-shaped setae medially and ventrally. Body and legs often with elaborate lamellae. . . . . . . *Agaue* Lohmann 1889; p. 183.
Cosmopolitan.

3b. Palpi nearly always distinctly geniculate (Fig. 145). (Lines drawn as above usually form an angle of more than 30° [ca. 20° in *H. anomalus*].) P-3 plus P-4 usually longer than P-2. Sides of rostrum in most (but not all) species distinctly convergent.

5a. P-3 with a medial seta which is usually spiniform, but which is rarely very slender (*Halacarus* s. lat.).

6a. I-4 very nearly as long as, or slightly longer than, either I-3 or I-5 (Fig. 124). . . . . *Halacarus* s. str. Gosse 1855; p. 81.
Cosmopolitan.

6b. I-4 distinctly shorter than either I-3 or I-5 (Fig. 171).
Subg. *Thalassarachna* Packard 1871; p. 100.
Apparently not tropical.

5b. P-3 without setae (*Copidognathus* s. lat.).

7a. I-1 with 3 setae ventrally [2 ventro-medially and 1 ventrally or ventrolaterally in deutonymphs and adults (Figs. 232, 251)]. Rosette pores usually present, but sometimes with porose panels. Marine; rarely in fresh water. . . . . *Copidognathus* s. str. Trouessart 1888; p. 129.
Cosmopolitan.

7b. I-1 with 2 pairs of ventral setae in deutonymphs and adults (Fig. 312). Rosette pores absent. Marine or brackish water.
Arhodeoporus, new subgenus; p. 173.
Apparently not tropical.

Subfamily Porohalacarinae Viets 1933

1a. I-4 as long as, or nearly as long as, I-3 and I-5.
Lobohalacarus Viets 1939.
Europe, South America.

1b. I-4 appreciably shorter than I-3 and I-5.

2a. Medial member of the ring of 3 setae on base of P-4 short, spine-like.
Troglohalacarus Viets 1937
Spain.

2b. All 3 setae at base of P-4 long, slender.

3a. Anal opening terminal. One pair of internal genital suckers present.
Caspihalacarus Viets 1928.
Caspian Sea.

3b. Anus subterminal. Only external genital suckers present, and variable in number. . . . . *Porohalacarus* Thor 1923.
North America,[6] Europe, Africa.

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[6] First record.

Subfamily LOHMANNELLINAE Viets 1927

1a. External genital suckers. Fresh water. . . . .*Porolohmannella* Viets 1933.
North America,[7] Europe,
Asia.

1b. Internal genital suckers only. Marine or brackish water.

  2a. Capitulum sometimes very long, but only ⅙ to ⅓ as wide as body. Rostrum of uniform width beyond middle, rounded terminally, not broadened (dorsal view). Marine or brackish water.
Lohmannella Trouessart 1901; p. 190.
Possibly cosmopolitan, but not yet
recorded from tropical waters.

  2b. Capitulum grotesquely enlarged; base of capitulum nearly, or more than half, as broad as body. End of rostrum considerably broadened, wider than middle portion of rostrum (dorsal view). Marine.
Scaptognathus Trouessart 1889.
Ireland, English Channel,
France.

Subfamily SIMOGNATHINAE Viets 1927

1a. I-6 reduced to a short clawless stump. Basal portion of I-5 more slender than distal end, widening abruptly a little beyond basal end (*i. e.*, I-5 pedunculate). Highest portion of I-5 proximal to middle of that segment. I-5 with only slender setae. Ocular plates absent. Palpi contiguous basally. (Known from only two specimens of the genotype.)
Acaromantis Trouessart *et* Neumann 1893.
French Atlantic coast.

1b. I-6 with 2 heavy claws. I-5 pedunculate or not, but with highest portion of segment at, or beyond, middle. I-5 also with a heavy ventral seta at level of maximum height. Ocular plates present or absent.

  2a. I-5 highest at middle of segment, so that the ventral seta does not reach as far as the claws on I-6 but would contact this segment at a point proximal to the base of claws. I-6 (including claws) slightly longer than I-5. (Known from a single female.) Profundal (1410 meters). . . .*Atelopsalis* Trouessart 1896.
Bay of Biscay.

  2b. I-5 highest at distal end, so that the heavy ventral seta is displaced distally and is opposable to the claws on I-6 when the latter is flexed. I-6 (including claws) slightly shorter than I-5.

    3a. Epimera III and IV contiguous (as seen in ventral view).
Simognathus Trouessart 1889.
Mediterranean, Caribbean,
North Sea.

    3b. Epimera III and IV separated by a thin band of striate cuticle,
Ischyrognathus Trouessart 1900.
Western Indian Ocean.

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[7] First record.

Subfamily LIMNOHALACARINAE Viets 1927[8]

1a. Claws on I-6 with a distal mushroom-like expansion which bears peripherally about 8 to 10 teeth directed parallel to stalk of claw (*i. e.*, the teeth curve back sharply toward the base of the claw)...... (*Soldanellonyx* s. lat. Walter 1917.)

  2a. P-I attached proximally to P-2 in the normal manner; axis of palp not forming a right angle between P-1 and P-2. Rostrum (as seen from above) slender, conical, pointed. Palpal insertions not elevated dorsally above base of capitulum. Chelicera distinctly 2-segmented, the movable digit distinct from base of claw. I-3, I-4 and I-5 of essentially the same dorso-ventral height. Fresh water.................. *Soldanellonyx* s. str. Walter 1917.
  Europe, North America, Java.

  2b. P-1 attached basi-ventrally to P-2, so that axis of palp forms somewhat of a right angle between these two segments. Rostrum (as seen from above) wide at base and broadly triangular. Palpal insertions on tubercles which are elevated well above dorsal surface of base of the capitulum. Chelicerae dagger-like, the movable digit not distinct from the basal portion. I-3 and I-5 greatly swollen, much higher than I-4.
  Subg. *Parasoldanellonyx* Viets 1929.
  Europe, British Isles.

1b. Claws on I-6 without such a mushroom-like expansion. Claws more or less pectinate, but the pecten is a straight comb.

  3a. P-3 without heavy seta disti-ventrally. Claws with extremely fine comb and without accessory tooth..................... *Hamohalacarus* Walter 1931.
  North America.

  3b. P-3 with heavy seta disti-ventrally. Claws distinctly pectinate. (*Limnohalacarus* s. lat. Walter 1917.)

    4a. Only III-5 with 2 ventral, widely separated, finely pectinate setae. P-1 dorso-ventrally much lower than P-2 and oriented at right angles to P-2. P-2 with a long disti-dorsal seta and a shorter seta more basally.
    Limnohalacarus s. str. Walter 1917.
    North America,[9] South America.

    4b. I-5 to IV-5 each with a pair of disti-ventral, flattened, coarsely-toothed setae. P-1 as high as P-2 and oriented along the same axis (not at right angles). P-2 with a short seta disti-dorsally as well as basally.
    Subg. *Stygohalacarus* Viets 1934.
    Yugoslavia.

Subfamily HALIXODINAE Viets 1927

Represented by a single genus. See characters in key, p. 19. Parasitic on gills of chitons............................. *Halixodes* Brucker and Trouessart 1900.
New Zealand.

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[8] This is a close translation of Viets' key (1934a: 138).

[9] First record.

Subfamily ENTEROHALACARINAE Viets 1938

Represented by a single genus. See characters in key, p. 19. Parasitic in gut of sea urchins. . . . . *Enterohalacarus* Viets 1938.
Western Pacific (Sulu Sea).

Subfamily ASTACOPSIPHAGINAE Viets 1931

Represented by a single genus. See characters in key, p. 19. Parasitic on gills of *Astacopsis* (Crustacea, Decapoda). . . . . *Astacopsiphagus* Viets 1931.
Australia.

SYSTEMATIC AND NOMENCLATORIAL NOTES ON THE SUBFAMILIES AND GENERA

Porohalacarinae Viets 1933. The family Porohalacaridae of Viets has been combined with the Halacaridae, since this is a more natural arrangement than that heretofore employed. It is obvious that *Porolohmannella* should never be allied with *Porohalacarus* and at the same time separated from its direct relative, *Lohmannella*, for these two genera are so close that the writer does not believe the presence of external genital suckers is sufficient grounds for even a subfamilial distinction. It seems more important from a systematic standpoint to express the fundamental morphological likeness of these two genera than to point out special ecological adaptations. Accordingly, the subfamily Porolohmannellinae Viets 1933 is made a synonym of Lohmannellinae Viets 1927. Viets' distinction between Halacaridae and Porohalacaridae is, in the final analysis, strictly ecological (see Viets 1940g: 114), without regard to natural lines, and the Porohalacaridae should therefore be abandoned as a taxonomic group.

Both the subfamilies Porohalacarinae and Limnohalacarinae will require further internal reorganization as the relationships between the various genera are more clearly established and the relationships to other groups in the Halacaridae are determined. However, at present this is not possible owing to our limited knowledge of most of the genera.

Rhombognathinae Viets 1927. The revision of the Rhombognathinae is also made with a view to expressing fundamental relationships between groups of species which underlie superficial specific differences. Viets (1927a: 97–115) divided *Rhombognathus* Trouessart 1888 into three subgenera on the basis of claw characters: *Rhombognathus* s. str. Trouessart 1888 (two claws on all tarsi; type, *R. notops*

[Gosse] 1855), *Rhombognathides* Viets 1927 (three claws on I and II; two on III and IV; type, *R. pascens* [Lohmann] 1889) and *Rhombognathopsis* Viets 1927 (three claws on all tarsi; type, *R. seahami* [Hodge] 1860).

For several years it has been apparent that this grouping may lead to difficulty in the case of *Rhombognathus pascens* (Lohmann) 1889. *R. pascens* (= *Aletes pascens*) was described as having a median claw on only legs I and II, and it was so considered until 1935. Schulz (1935a: 86) noted in Helgoland material two specimens which had a median claw on all legs, which according to Viets' characterization would make this a *Rhombognathopsis.* However, since the other characters indicated that these were *R. pascens,* Schulz considered them simply a variety of this species (no name was given). However, Schulz did not discuss the significance of the occupation of two subgenera by the type of *Rhombognathides.* Viets (1939c: 534) considered that Schulz actually had specimens of *Rhombognathus mucronatus,* but there seems to be no way of proving this, unless Schulz still has his specimens. Viets stated more positively (1940g: 110, footnote) "Abzustreichen ist *Rhombognathides pascens* var. Schulz 1935; es hat sich herausgestellt, dass darin *Rhombognathopsis mucronatus* Viets vorliegt." But Viets again did not substantiate this statement in any way. However, even if it were true the other grounds for the revision of *Rhombognathides* are adequate.

The extremely close similarity between *pascens* and *seahami* is further evidence that the subdivision of *Rhombognathus* s. lat. on the basis of claw characters alone is unnatural. It is inconceivable that such similarity could have arisen by convergence of two naturally distinct groups, and it is also inconceivable that *R. seahami* could be more closely related to *Rhombognathus* (s. lat.) *armatus* than to *R. pascens,* as its present nomenclatorial position does indicate.

Finally, the present writer has found a species on the North American coast which is represented by two distinct varieties, distinguishable only on the basis of claw characters. One of these (*R. merrimani merrimani,* n. sp., n. var.) would go in *Rhombognathus* s. str.; the other (*R. m. needleri,* n. sp., n. var.) would go in *Rhombognathides* as these are now defined by Viets. This, of course, is an illogical situation.

Rhombognathides, as defined by Viets (1927–1940), therefore overlaps both *Rhombognathopsis* and *Rhombognathus* s. str. Even if this were not the case the subgeneric separation of certain species (including the types) of these two nomenclatorial groups is unnatural.

However, natural groups do exist within the *Rhombognathinae*. *R. pascens*, *seahami*, *trionyx*, *merrimani*, n. sp., and *mucronatus* are quite different from other species in certain respects (e. g., *notops* [Gosse], *longirostris* Trouessart and *peltatus* Viets). One fundamental difference between these two groups is the form and position of the female genital opening. In *R. pascens* this opening is terminal and ventral to the anus and is covered by a pair of heavy, cusp-like opercula. In other species the genital opening of the female is anatomically, as well as morphologically, anterior to the anus and is guarded by a pair of simple, band-like sclerites at the most. *Rhombognathus* (s. lat.) *armatus armatus*, *armatus americanus* and *nudus* differ in several respects from species of both *Rhombognathus* and *Rhombognathides*, and merit generic distinction. The species *setosus*, *levis* and *hutchinsoni*, n. sp., form a natural group which may also include *magnus*. For these reasons it is necessary and desirable to revise the *Rhombognathinae*.

This case somewhat resembles that found in a number of the Oribatoidea in which mono-, di- and tridactyle forms are found within a single species, as for example *Scheloribates praeincisus* Berlese 1910 (see Willmann 1931b: 271–272). It has long been recognized by workers in the Oribatoidea that the number of claws is completely unreliable as a generic character and that in many cases it does not have even specific value.

It appears likely that positive identification of larvae can be made on the basis of the bacillum and prebacillum, since these structures have been found constant throughout the development of the few species for which all stages are available. Observations on the condition of the genital and anal plates will probably reveal that nymphs also can be easily segregated into their proper genera. Because of the fact that all larvae and nymphs will probably be shown to be distinguishable generically, and since the various differential characters are quite fundamental, the subfamily will hereafter be considered as containing four distinct genera.

Rhombognathus Trouessart 1888. In this genus are retained those forms which are congeneric with the type, *R. notops*, and provisionally those which cannot yet be placed in the other genera because of inadequate descriptions. The ventral armor of the adults is completely or almost completely fused, the genital opening of the female is ventral, and although the band-like sclerites may be relatively broad, they are not cusp-like. The deutonymph has the genital and anal plates separated. In the forms seen by the writer the carpite was (apparently) not fused to the end of the tarsus and the shaft was straight and without a moniliform structure. The end of the tarsus is without a ventral seta. The bacillum is very rudimentary on I-6 and absent on II-6; the prebacillum is very long and slender. The parambulacral setae on I-6 and II-6 are divaricate. The genital and anal plates of the nymphs are separate.

Type. *R. notops* (Gosse) 1855.

With the removal of four species to the new genus *Isobactrus*, *Rhombognathus* is now left with the following:

1. *notops* (Gosse), 1855 (genotype).
2. *magnirostris magnirostris* Trouessart 1889.
3. *magnirostris plumifer* Trouessart 1889.
4. *magnirostris lionyx* Trouessart 1900.
5. *magnirostris praegracilis* Viets 1939.
6 *sphaerorhynchus* Police 1909.
7. *pectinatus* Viets 1936.
8. *peltatus* Viets 1939.
9. *parvulus* Viets 1939.
10. *apsteini* Lohmann 1907.
11. *intermedius* Schulz 1933.
12. *uniscutatus* Viets 1939.
13. *spinipes* Viets 1933.

That the first ten of these are congeneric is certain, although the distinctions between them have not been adequate in some cases. These ten must be restudied thoroughly to determine the relative importance of the characters on which the species and subspecies are based and the degree of variability that occurs in these characters. It is most probable that some of the species are really no more than varieties of *R. magnirostris*, or that some of the latter should be considered as distinct species. The writer has seen only two of this group and cannot make any contribution to their revision.

R. spinipes certainly is not congeneric with the first ten. It shows characters that ally it to *Rhombognathides* or possibly *Metarhombognathus*, but the description (based only on the deutonymph) does not allow positive disposition of the species. It is not related to *Isobactrus levis*, nor to any other *Isobactrus*, despite the smooth claws! Viets (1933d: fig. 9a, b) showed a bacillum and a prebacillum on I-6 and a bacillum on II-6, which are relatively long.

R. uniscutatus shows very significant differences from the first ten. Its closest relatives lie in *Isobactrus* or *Metarhombognathus*, but its true position is not ascertainable at present. It is not a *Rhombognathus*.

The description of *R. intermedius* is not adequate to permit certain placing of the species. It is not clear from either the description or the figures given by Schulz just what the true structure of the ventral surface is, but Viets (1939d: 530–531) placed this species in the group with all ventral plates fused (i. e., *Rhombognathus*). This appears logical to the present writer in view of the number and arrangement of the setae around the genital opening, which is similar to that found in species of *Rhombognathus* and quite unlike that found in the other genera.

Rhombognathus magnipalpus Viets (1928a: 13) is a *lapsus calami* for *magnirostris*, and hence it is a synonym of *R. magnirostris magnirostris*.

Aletes gracilis Lohmann 1893 is a synonym of *Rhombognathus notops* (Gosse). The name was a provisional one to be applied in the event the Baltic form should eventually be shown to be distinct from the British form. Subsequent workers have considered them identical.

Rhombognathides Viets 1927, emended. In this genus the genital opening of the female is terminal and is guarded by a pair of large, cusp-like opercula. The armor is usually heavy. The claws are angularly bent and pectinate, or scythe-shaped, and with or without accessory tooth. Two claws are present on all tarsi, or three on I and II and two on III and IV, or three claws on all tarsi. I-6 and II-6 have only the bacillum, which is long and rod-shaped and more than five times as long as thick in the forms known to the writer. In the nymphs the genital and anal plates are completely fused.

Synonym. *Rhombognathopsis* Viets 1927 (genotypes congeneric, and *Rhombognathides* has line precedence [Viets 1927a: 88, line 5] over *Rhombognathopsis* [Viets 1927a: 88, line 6]).

Type. *Rhombognathides pascens* (Lohmann) 1889, by original designation.

Eight species, one of which is represented by two varieties, can be assigned to *Rhombognathides*. Of these *Rhombognathides pascens*, *seahami*, *mucronatus*, *trionyx* and *merrimani*, n. sp., are well known and adequately described. *Rhombognathides exoplus* has not been well described, although apparently it is a valid species; but *Rhombognathides nigrescens* and *minutus* are open to considerable question. The latter two are almost certainly not distinct species, and the recorded habitat of *R. nigrescens* (Crag Lake, Northumberland, England) is probably erroneous. The key given here includes the two apparently nominal species as well as the six which are valid. A separate key to the North American species is given on page 47.

1a. Lateral claws pectinate.
  2a. Fresh water. (Median claw on all legs.) Length 700μ.
    nigrescens (Brady) 1877.
    England (Northumberland, Crag Lake?).
  2b. Marine.
    3a. Ocular plates with 2 corneae. Minute median claw on all legs.
      exoplus Trouessart 1901.
      English Channel (France).
    3b. Ocular plates with 1 cornea.
      4a. Median claw on all legs, ¾ as long as lateral claws. Setae surrounding genital area of male reaching to or beyond middle of GA. A pair of setae in the membranous area between AD and PD.
        mucronatus Viets 1927; p. 54.
        North Sea, North America.
      4b. Median claw on all legs, or only on I and II; only ½ as long as lateral claws. Setae surrounding genital area of male not reaching to middle of GA. All dorsal setae included within the plates.
        5a. Median claw on only legs I and II (except Schulz 1935?). Body 300–360μ long.................. *pascens* (Lohmann) 1899; p. 48.
          Black Sea, French Atlantic coast, North Sea, Baltic, England, Ireland, North America.
        5b. Median claw on all legs. Body 360–420μ long (but usually distinctly longer than *pascens*)............... *seahami* (Hodge) 1860; p. 51.
          Baltic, North Sea, French Atlantic coast, England, Ireland, North America.
1b. Lateral claws not pectinate; accessory tooth present or absent.
  6a. Lateral claws with accessory tooth. Known only as larva.
    minutus (Hodge) 1863.
    England (Seaham Harbor).
  6b. Lateral claws without accessory tooth.

7a. Two corneae present . . . . *trionyx* Trouessart 1900. Tierra del Fuego; French Atlantic coast.

7b. Single cornea present . . . . *merrimani*, new species; p. 56. North America (New Brunswick).

8a. All legs lacking median claw. *merrimani merrimani*, new species, new variety; p. 56.

8b. Legs I and II with median claw; III and IV with only the lateral claws. *merrimani needleri*, new species, new variety; p. 59.

Rhombognathides minutus (Hodge) 1863. Viets (1940g: 535) stated in his key, "5 (4). Larve! Seitenkrallen ohne Nebenzinke, sichelförmig, ohne Kamm . . . *minutus* (Hodge) 1863." But elsewhere (1927a: 107) he said, "Krallen einfach sichelförmig, ohne Kamm, mit Nebenzinke" which is correct. Hodge (1863: 11) clearly showed an accessory tooth. This species is very inadequately described, but clearly it is neither a *Metarhombognathus* nor a *Rhombognathus*, and since its claw characters do not exclude it from *Rhombognathides* it is placed in that genus.

Rhombognathides nigrescens (Brady) 1877. Although this has never been adequately described it apparently belongs in this genus. There is a median claw on the tarsi and the lateral claws are angularly bent and pectinate, as in *Rhombognathides pascens*, *seahami* and *mucronatus;* it is completely unlike any of the species in *Metarhombognathus*. Its true status is no clearer today than it was in 1877.

Rhombognathides exoplus (Trouessart) 1901. André's redescription (1939c: 312) of this species is apparently based on a male, although his drawing leaves some doubt about this. The general facies is that of a *Rhombognathides* species, however, and it is placed in that genus. It is not related to any of the *Metarhombognathus* species.

Rhombognathides seahami (Hodge) 1860. Since all workers after 1889 have recognized *R. seahami* of the British Isles as identical with that of the Baltic, *Aletes triunguiculatus* Lohmann 1889 (p. 326) is a synonym of *Rhombognathides seahami*. The name was a provisional one, advanced by Lohmann to be applied to the Baltic form in the event it should prove distinct from the British form.

Metarhombognathus, new genus. In this genus there are three very heavy, scythe-shaped claws (in forms known at present) on all tarsi, and the median claw is nearly as heavy as the lateral claws. The deutonymphs are more heavily armored than the adults. The genital opening of the female is subterminal and not guarded by cusp-like opercula. The epimeral plates are greatly reduced in the adult but normal in the deutonymphs. I-6 has both a bacillum and a prebacillum, but II-6 has only the bacillum; these are short and club-shaped and less than five times as long as thick. Genital and anal plates of the protonymph and deutonymph are undivided, but those of the adult are separated by a band of striate cuticle.

Type. *Metarhombognathus armatus* (Lohmann) 1893.

The known species of *Metarhombognathus* can be distinguished by the following key.

1a. Lateral claws bifurcate or trifurcate at end. Fourth pair of setae in dorsal series just in front of PD of deutonymph........*nudus* (Viets) 1928; p. 62.
Arctic Ocean (Kola Fjord).

1b. All claws simple and hook-like. Fourth pair of setae in dorsal series included in PD [*armatus* (Lohmann) 1893].

  2a. PD in deutonymph extending only to level of dorso-lateral setae of PE. Seta lateral to corneae lying in the membranous area. OC separated by a space greater than width of AD...*armatus armatus* (Lohmann) 1893; p. 60.
  North Sea.

  2b. PD in deutonymph extending beyond level of dorso-lateral setae of PE. Seta lateral to corneae lying in OC. OC separated by a space less than width of AD.........................*armatus americanus*, new subspecies; p. 60.
  North America.

Metarhombognathus armatus armatus (Lohmann) 1893. *Rhombognathopsis mollis* Viets 1927 is a synonym (see p. 60).

Metarhombognathus nudus (Viets) 1928. *Rhombognathopsis contectus* Viets 1928 is a synonym (see p. 62).

Isobactrus new genus. In this genus the genital opening of the female is ventral in position, not guarded by a pair of large, cusp-like opercula, and surrounded by only three pairs of setae. The adults are more heavily armored than the nymphs, but all dorsal and ventral plates are separate; the ventral plates are greatly reduced and do not form a solid plate. Femur I is greatly swollen and is less than 1.5 times as long as high. Tarsi I and II each have a single club-like seta in front of lateral disti-dorsal seta. (The generic name indicates the contrast between this condition and that in which there are two such setae—the bacillum and prebacillum—on I, but only the bacillum on II. Of course this is not the sole character on which the genus is based.) There are two claws on all tarsi of the known forms. Intertidal, feeding on algae; usually very agile forms.

Type. *Isobactrus setosus* (Lohmann) 1889 (= *Aletes setosus* Lohmann 1889).

The known species of *Isobactrus* can be distinguished by the key given below. A key to the North American species is given on page 69.

1a. Claws with a well developed comb which projects medially from the shaft of claw. (Note. When the claw is lying on its side, or somewhat obliquely, it may appear to have only an accessory tooth or even to be completely smooth.)
setosus (Lohmann) 1889; p. 69.
Connecticut, British Isles, French Atlantic coast, North Sea, Baltic.

1b. Claws completely smooth, or with a tooth on concave margin of claw near base (not to be confused with an "accessory tooth," which is absent).

  2a. Claws with basal tooth as above............. *magnus* (Lohmann) 1907; p. 33.
  Kerguelen.

  2b. Claws completely smooth.

    3a. Tarsus with a single long seta dorsally near middle of segment. Panelling very pronounced; PD with costae........*hutchinsoni*, new species; p. 77.
    Connecticut.

    3b. Tarsus with 2 long setae dorsally near middle of segment. Panelling present but rather feebly developed; costae absent from PD.
    levis (Viets) 1927; p. 74.
    Baltic; Connecticut.

Isobactrus magnus is placed in this genus provisionally, since it appears, on the basis of Lohmann's descriptions, to agree more closely with this genus than with any of the others. It appears to be somewhat different from the other species of *Isobactrus*, however, although the significance of the differences cannot be evaluated at present. Lohmann's drawings clearly showed a moniliform carpite.

R. cryptorhynchus Trouessart is a synonym of *R. setosus* (Lohmann), according to André. See discussion, page 71.

Agaue Lohmann 1889. The redefinition of *Agaue* Lohmann 1889 by Viets (1927a: 90–95) has been reviewed several times by Viets, André, and Womersley, and therefore it need not be discussed again here, except to say that the change was fully warranted on morphological and taxonomic grounds and is accepted in the present paper.

Copidognathus Trouessart 1888. Viets (1927a: 87, 91, 144) divided *Copidognathus* Trouessart into two subgenera on the basis of the form of the ocular plates. Those with elongate ocular plates, often with the posterior portion caudiform, were placed in the subgenus *Copidognathopsis*, while the others were left in *Copidognathus* s. str. As is often the case with purely relative diagnostic characters of this type, it might be supposed that as more and more species became known the distinction between the two subgenera would become more and more difficult, until eventually cases would arise in which closely related species were placed in different subgenera along with forms to which they were only remotely related. Such a discrepancy appears to exist in the case of *C. extensus* Viets 1940 (g: 37–39) and *C. pachypus*, n. sp. Although these species differ in many details, they also appear to be more closely related to each other than to any other species. According to Viets' most recent characterization of *Copidognathopsis*,[10] *C. pachypus* seems to be more of a *Copidognathopsis* than a *Copidognathus* s. str., and yet its closest relative appears to be *C. extensus*. It is certain that such ambiguities will only increase in the future if the present systematic arrangement is retained. In short, the form of the ocular plates may be a useful key character, but its use as a subgeneric character is more of an impediment than an aid in the taxonomy of the group. There is no doubt that the present arrangement serves to obscure fundamental characters on which to base a division of *Copidognathus*. The present writer regards *Copidognathopsis* Viets 1927 as a synonym of *Copidognathus* Trouessart 1888, because the characters upon which the genotypes have been separated are inadequate.

On the other hand, there is a group of species which formerly were placed in the subgenus *Copidognathopsis*, but which are distinct from all other species of *Copidognathus* in the number of ventral setae on tibia I. The other species of *Copidognathus* are remarkable for the apparently absolute constancy of the number (three) and arrangement (two ventro-medial; one ventral or ventro-lateral) of the ventral setae on the first and second tibiae. But in *C. arenarius*, n. sp., *C. submarinus*, n. sp., *C. gracilipes gracilipes* (Trouessart) 1889, *C. gracilipes quadricostatus* (Trouessart) 1894 and *C. gracilipes largiforatus* (Trouessart) 1899 there are two pairs of ventral setae on I-5 in both the deutonymph and the adult. These five forms are clearly more closely related to each other than to any other species in the genus and therefore form a distinct and natural species group. All have a short, blunt rostrum which extends only a little beyond the middle of P–2, and apparently all lack rosette pores on any of the plates. The above five forms are removed to *Arhodeoporus*, n. subg. The name indicates the absence of rosette pores, but this is not the most important character on which the subgenus is based. Furthermore, not all "arhodeoporose" species belong here.

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[10] Viets (1940g: 52) stated, "Die Okularia sind hinten in eine schmale Spitze ausgezogen, oder bandartig verlangert, und mehr als zweimal so lang wie breit."

Werthella Lohmann 1907 is herein synonymized with *Copidognathus* s. str. because its type is a *Copidognathus* s. str. The species that have been described in the genus are also *Copidognathus* species. Lohmann (1907a: 390), in his diagnosis of the genus, stated (translation),

> Especially characteristic of *Werthella* are the short maxillary palpi which are widely separated at the base by a broad epistome, but which come together over the chelicerae so that the distal ends of the thick second segments nearly, or almost nearly, touch. The body is flat and broad, the legs graceful and short. Leg I is somewhat heavier than the others, but in other respects is no different. The capitulum consists of a short, compact basal portion and a triangular, basally broadened rostrum. Palpi distinctly four-segmented, short, and heavy. Segment 2 is especially thick, but the terminal segment is nearly cylindrical, with a short, stylus-like point. Chelicerae two-segmented with a typical 'claw'. Tarsal claws attached to legs only by a 'Krallenmittelstückes.'[11] A claw fossa is well developed.

Since the genus is obviously closest to *Copidognathus* it is necessary to compare it only with that genus. All but the first sentence in the above translation could be applied to any typical *Copidognathus* species. An examination of Lohmann's plate 31, fig. 9, shows that the chaetotaxy of I-5 is identical with that of all *Copidognathus* s. lat. species with the exception of *C. gracilipes*, *arenarius* and *submarinus* (which certainly deserve subgeneric distinction). In all species except these three, I-5 has three heavy setae on the ventral and medial surfaces, as is the case in Lohmann's species.

Turning to the characters in the first sentence of the translation, then, it is apparent that these are also inadequate to merit even subgeneric distinction for *Werthella*. The approximation of the palpi dorsally is shown exceptionally well (even more strikingly than in *Werthella parvirostris*!) in Lohmann's plate 41, fig. 1 (*Copidognathus* [s. str.] *simonis*). This condition shows up occasionally in individuals of many species of *Copidognathus*, for example, *C.* (s. str.) *bairdi*, n. sp., and C. (s. str.) *punctatissimus* (Gimbel), *etc.* Therefore this character has no generic value, since it cannot be applied in practice even as a specific character. That leaves only the shortness of the palpi, which is quite probably as much apparent as real and in any event is only a specific character, since there are no structural changes associated with it. It is due in part to the sharply dorsad course of P-2, although the palpi apparently are really smaller than usual. However, the size of the palpi is not even a critical *subgeneric* character, for reduction in size could occur, and undoubtedly has occurred, at several points within the genus *Copidognathus*. Hence, *Werthella parvirostris* (Trouessart) is only a *Copidognathus* s. str. with relatively short palpi, and *Werthella* is therefore made a synonym of *Copidognathus* s. str.

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[11] That is, without a carpite.

Trouessart (1914a: 6–8) described a second species, *Werthella bouvieri*, in which the convergence of the palpi is completely lacking, the palpi being shown as parallel. The palpi are relatively short, but it is also apparent that the rostrum is of unusual length, it being appreciably longer than the base of the capitulum. But there are no morphological differences whatever between the capitulum of this species and that of other species of the genus *Copidognathus*. Therefore, *Werthella bouvieri* Trouessart 1914 is a synonym of *Copidognathus bouvieri* (Trouessart) 1914. Either Trouessart's drawing or his measurements are inaccurate. The total length of his fig. 3 is 60 mm. (to tip of rostrum) and the width is 35 mm. (L/W = 1.71). But Trouessart's measurements (700/350µ) give a ratio of 2.0—a significant difference. Other errors in the drawings are indicated by Trouessart on page 16 of his paper.

Copidognathus (s. str.) *curassaviensis* Viets 1936 is also a form in which the palpi are relatively small. P-3 and P-4 combined scarcely equal the length of P-2, and the rostrum extends beyond P-3. But this form is a typical *Copidognathus* species and there are no valid morphological grounds on which it could be removed from that genus. Viets was correct in placing it in *Copidognathus*.

For the same reasons outlined above, *Werthella johnstoni* Womersley 1937 is a synonym of *Copidognathus johnstoni* (Womersley) 1937. The elimination of *Werthella* is dictated on morphological grounds, but its elimination is also advisable for purely practical reasons, for it would be impossible to define the point which made a particular species either a *Copidognathus* or a *Werthella*. Post-mortem differences in the attitude of the palpi in different specimens have been, and would be, misleading, and differences due to preparation would introduce still more difficulties into the taxonomy of a genus which is already the largest in the family. Confusion must be eliminated everywhere possible if chaos is to be avoided.

Halacarellus Viets 1927. The elimination of *Halacarellus* has been discussed in detail by the present writer (1945a) and need not be reviewed here (see also p. 100).

Simognathinae Viets 1927. As Viets has already pointed out (1927a: 95–96), the subfamily Simognathinae Viets 1927 contains four genera of uncertain relationship. This uncertainty is principally due to the rareness of their representatives. Trouessart is the only one who has done any completely original work on the genera *Acaromantis*, *Atelopsalis* and *Ischyrognathus*, and his descriptions are inadequate in several fundamental details, although they would permit recognition of the forms. Each of these three genera is represented by a single species and apparently by no more than two specimens of each at most. André's (1938b: 170–172) restudy of Trouessart's type specimen of *Ischyrognathus coutieri* still leaves much to be desired. Obviously new material is necessary. There seems to be no reason for separating it from *Simognathus*, either generically or subgenerically. The genus *Simognathus* is well known through the work of Viets (1936d, 1940g). The genus *Atelopsalis*, known from only a single female, is too superficially described to properly evaluate its systematic position. Trouessart's figures (drawn by Neumann), although relatively good, show considerable evidence of having been drawn from a compressed specimen. Thus the position of the attachment of the palpi may have been altered. Also, the position of the palpi is not favorable for study, so that it cannot be safely assumed that these are three-segmented, as claimed by Trouessart. Although the genera of Simognathinae appear to have (on the basis of published descriptions) certain differences, they also have several points of similarity, the relative importance of which cannot be evaluated at present. Accordingly, it is best to leave them as they now stand until further work can be done.

SUMMARY OF HALACARIDAE MURRAY 1876

Those genera or subgenera which are marked by an asterisk are known to be present in North America. A double asterisk indicates those which are herein recorded for the first time, but which, being fresh-water genera, will not be treated in detail in this paper (see keys on pages 20–25).

Subfamilies	_Genera_	_Subgenera_
Rhombognathinae	*_Rhombognathus_	
	*_Rhombognathides_	
	*_Metarhombognathus_, n. gen.	
	*_Isobactrus_, n. gen.	
Actacarinae	_Actacarus_	
Halacarinae	*_Halacarus_ s. lat.	*_Halacarus_ s. str.
		*_Thalassarachna_
	*_Copidognathus_ s. lat.	*_Copidognathus_ s. str.
		*_Arhodeoporus_ n. subg.
	*_Agaue_	
	*_Agauopsis_	
	Coloboceras	
	Pontacarus	
Porohalacarinae	**_Porohalacarus_	
	Caspihalacarus	
	Lobohalacarus	
	Troglohalacarus	
Lohmannellinae	*_Lohmannella_	
	**_Porolohmannella_	
	Scaptognathus	
Simognathinae	_Simognathus_	
	Ischyrognathus	
	Acaromantis	
	Atelopsalis	
Limnohalacarinae	*_Soldanellonyx_ s. lat.	*_Soldanellonyx_ s. str.
		Parasoldanellonyx
	*_Limnohalacarus_ s. lat.	**_Limnohalacarus_ s. str.
		Stygohalacarus
	*_Hamohalacarus_	
Halixodinae	_Halixodes_	
Enterohalacarinae	_Enterohalacarus_	
Astacopsiphaginae	_Astacopsiphagus_	

Soldanellonyx and _Hamohalacarus_ were first recorded from North America (Indiana) by Walter, 1931a.

THE NORTH AMERICAN MARINE HALACARIDAE

Included here are descriptions of the genera, species, subspecies and varieties of the North American marine Halacaridae which have been taken by the writer. In some cases in which previous descriptions of the species have been adequate only the records of capture and miscellaneous notes on the anatomy are given. Keys to the North American species of the genera are provided except where only one or two are known. For definitions of the morphological terms employed, or references to labelled figures, see pages 222 to 226. The bibliographical lists contain references to only those papers which have an important bearing on the nomenclature or systematics of the genus or species involved, or in which good figures or descriptions are available, but all known synonyms of the genus or species are included.

Subfamily Rhombognathinae Viets 1927

Diagnosis. Middle piece of claw articulating with carpite, which in turn articulates with, or is fused with, end of tarsus. Palpi very small, 4 or 3-segmented, closely appressed to sides of rostrum. All dorsal plates present and occasionally fused to form a single dorsal plate, in which case corneae are present. Predominantly marine and intertidal. Never surviving under conditions which preclude algal growth, and rarely, if ever, in fresh water. Cosmopolitan.

Genus *Rhombognathus* Trouessart 1888

Trouessart 1888a, 754: *Rhombognathus* new genus. Lohmann 1889a, 270–272, 276, 278, 319–334, etc.: *Aletes*, new genus. Lohmann 1901a, 276, 279–281, 335: *Rhombognathus.* Trouessart 1901c, 151: *Rhombognathus.* Viets 1927a, 88–89, 97–106, etc.: *Rhombognathus* s. str. Trt. 1888. Viets 1927b, 5–11, 39: *Rhombognathus* s. str. Trt. Viets 1939c, 528, 530–535, 545: *Rhombognathus* s. str. Trt.

Diagnosis. Genital opening of female ventral, not terminal, and guarded by a pair of band-like genital sclerites which may be broad but which are not cusp-like. Ventral armor of adults completely or almost completely fused. Deutonymph and protonymph with genital and anal plates separated. Carpite *apparently* not fused to end of tarsus (Figs. 1, 11), the shaft straight, without moniliform structure. End of tarsus lacking ventral seta. Bacillum very rudimentary on I-6 and absent on II-6; prebacillum very long and slender. Parambulacral setae on I-6 and II-6 divaricate.

Type. *Rhombognathus notops* (Gosse) 1855 (= *Pachygnathus notops* Gosse 1855), by original designation.

Remarks. Neither Lohmann nor any subsequent worker designated a type for *Aletes* Lohmann 1889. Although *Aletes* is unavailable for either of the new genera of Rhombognathinae established in this paper,[12] it is desirable to designate a type in order that its true status can be established. All writers since 1889 have listed *Aletes* Lohmann as a synonym of *Rhombognathus* Trouessart 1888. Accordingly, the present writer designates *Rhombognathus notops* (Gosse) 1855 (also type of *Rhombognathus*[13]) as type of *Aletes* Lohmann 1888. This was the fifth species listed by Lohmann, but to name any other would introduce needless confusion, since it would invalidate all previous statements regarding the synonymic status of *Aletes* Lohmann. *Aletes* Lohmann 1889 is a synonym of *Rhombognathus* Trouessart 1888 because their genotypes are identical, and *Rhombognathus* has priority.

KEY TO NORTH AMERICAN SPECIES (ADULTS)

1a. All dorsal plates separate. Base of capitulum readily visible in dorsal view and not concealed by AD. Setae postero-medially from corneae lying in CC and not in the membranous area. Each OC with 2 corneae. Claws completely smooth, without accessory tooth or fan-like lamella bearing a row of teeth along distal margin. . . . . *magnirostris lionyx* Trouessart 1900; p. 45.
North Carolina. Also Adriatic, English Channel, North Sea, Spitzbergen, Pacific-Antarctic (Macquarie Islands).

1b. As above, but claw not completely smooth, with at least one accessory tooth.
  2a. Claws (ventral or dorsal view) with only one accessory tooth. PD not reaching between OC. *notops* (Gosse) 1855; p. 41.
  Greenland, Great Britain, Baltic, French Atlantic coast.
  2b. Lateral claws (in ventral view) with a fan-shaped lamella along dorsal and inner edge of claw, which bears a row of 5 to 20 teeth along its distal margin. . . . . *magnirostris magnirostris* Trouessart 1889; p. 41.
  Florida; Chesapeake Bay. Also French Mediterranean, Adriatic, Black Sea, English Channel, North Sea.

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[12] The name *Aletes* was used three times prior to 1888, by F. Chapuis, 1874, Coleoptera, Chrysomelidae; C. Rafinesque, 1815, Lepidoptera, Pyralidae; P. Carpenter, 1856, Gastropoda.

[13] According to the international rules of zoological nomenclature, types of other genera are not to be excluded from consideration in establishing the type of a genus. The present case is an example of the value of this provision in avoiding unnecessary nomenclatorial changes.

Rhombognathus notops (Gosse) 1855

Gosse 1855a, 305–306: *Pachygnathus notops,* new species. Trouessart 1888a, 754: *Pachygnathus notops* Gosse (genotype of *Rhombognathus,* new genus); *Rhombognathus longirostris,* new species. Lohmann 1889a, 271, 316, 330–333, etc.: *Aletes notops* (Gosse) 1855; 333: *Aletes gracilis* (a provisional name). Kramer 1897a, 77, 83: *Rhombognathus notops* (Gosse). Lohmann 1901a, 279, 281–283: *Rhombognathus notops* (Gosse) 1855. Trouessart 1901a, 252: *Rhombognathus notops.* Viets 1927a, 89, 97–101, 152–153, 155–156, 159–161, 169–171: *Rhombognathus* (*Rhombognathus*) *notops* (Gosse) 1855. Viets 1927b, 8, 10, 32, 34, 53–55: *Rhombognathus notops* (Gosse) 1855.

Remarks. This species was reported from the west coast of Greenland by Kramer in 1897, the locality being given as Sermilik Fjord. It has not been seen by the present writer.

Rhombognathus magnirostris var. *magnirostris* Trouessart 1889

Figures 1–11

Trouessart 1889b, 181: *Rhombognathus magnirostris,* new species. Trouessart 1894b, 141, 153: *Rhombognathus magnirostris* Trt. Lohmann 1901a, 283: *Rhombognathus magnirostris* Trt. 1889. Trouessart 1901a, 250: *Rhombognathus magnirostris* Trt. Viets 1927a, 98–101, 153–154, 166, 168–171: *Rhombognathus* (s. str.) *magnirostris* Trt. 1889. Viets 1927b, 7, 8, 10–11, 47, 52–55: *Rhombognathus magnirostris* Trt. 1889. Viets 1928a, 5–11, 13: *Rhombognathus magnirostris* Trt. 1889; *p.* 13: *Rhomb. magnipalpus.* Viets 1939c, 532, 535–541: *Rhombognathus* (s. str.) *magnirostris magnirostris.*

Specimens obtained from Florida agree more closely with descriptions of this than with the descriptions of any of the other varieties of *R. magnirostris.* The author has only one intact female, which is 298μ long and 197μ wide. Thus it is identical in length with *R. pectinatus* Viets 1936 (Caribbean Sea) and shorter than any other recorded specimens of *R. magnirostris magnirostris,* which range from 380 to 450μ.

Female. AD 101 x 106μ, OC 83 x 56μ, and 85 x 58μ, OC-OC 58μ, AD-PD 30μ. Membranous areas more restricted than in *R. pectinatus* or *R. magnirostris magnirostris* (as described by Viets), but less restricted than in *R. magnirostris praegracilis* Viets 1939. OC with 2 pairs of setae and 3 pairs of lateral pores. Two pairs of perforated corneae present. PD with a pair of setae antero-laterally. A short and a long seta on AE just behind leg II on each side. Three lateral setae anterior to leg III, the most anterior one ventral, the second and third dorsal, and the third seta shortest. Dorsal plates with a small amount of conchoidal panelling as shown in Fig. 2.

Capitulum (Fig. 4) 79μ long to tip of rostrum and 62μ wide. Rostrum not sharply demarcated from base of capitulum. Two pairs of setae at the swollen middle of rostrum (anterior pair difficult to find). Palpi 4-segmented. Capitulum readily visible from above, the tips of palpi extending to, or a little beyond, middle of I-3 when the latter is extended anteriorly (Fig. 2). (The writer finds it impossible to interpret Viets' [1939c: 532] purely relative character "Stirnrand des Prädorsale das Capitulum fast vollig, kapuzenartig deckend," which he uses to differentiate *R. pectinatus* from all other *Rhombognathus* species.)

Chaetotaxy of legs:

	I				*II*				*III*				*IV*			
	d.	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*
1.	–	–	–	1	–	–	–	1	–	1	–	–	–	–	–	–
2.	1	1	–	–	1	1	–	–	1	1	–	–	1	1	–	–
3.	4	2	–	–	4	2	–	–	3	–	–	–	3	–	–	–
4.	2	1	1	1	3	1	1	1	1	1	1	–	2	1	–	–
5.	2	1	1	1	2	1	1	1	2	2	–	1	2	1	1	1
6.	3	–	–	–	3	–	–	–	4	–	–	–	3	–	–	–

In a female of unknown body length the following measurements were obtained:

	1+2	*3*	*4*	*5*	*6*	*Ambul.*	*Total*
I	30μ	60/34	26	48/26	51	32	247
II	30	63/31	26	48/25	51	32	250
III	47	53	26	47	59	42	274
IV	48	54	26	47	60	41	276

I-3 and I-5 1.77 and 1.85 times as long as high (swollen). The chaetography agrees closely with that shown by Viets (1939c: 536). Ventral and medial setae of I-5 pectinate. I-6 with bacillum greatly reduced and appearing as a mere stub; prebacillum very long and slender. Parambulacral setae divaricate. Ventral setae absent. II-3 and II-5 2.16 and 1.92 times as long as high. II-5 and III-5 with only the medial setae pectinate. II-5 with bacillum absent;

prebacillum very long and slender; parambulacral setae divaricate. III-6 with 4 setae dorsally, rather than the 3 found on all other tarsi (shown also by Viets). The disti-dorsal setae of the tarsi show an irregular tendency to be faintly pectinate. Parambulacral setae reduced to a single rod-shaped seta medially and a spine-like seta laterally. III-5 with ventral and medial setae pectinate, as on I-5. Parambulacral setae represented by a pair of spine-like setae which may or may not be pectinate (more accurate obervation not possible due to inadequate material). Claw fossa weakly developed and membranes absent. The distribution of the pectinate setae in the Florida specimens, as well as in European specimens described by Viets (1927a: 101), Trouessart (1889a: 231; "troisième article" should read "5^{e} article"), and in *R. pectinatus*, is given here in tabular form (S = smooth, P = pectinate, X = no seta found in this position):

	I		*II*		*III*		*IV*	
	4	*5*	*4*	*5*	*4*	*5*	*4*	*5*
Ventro-lateral	S	P	S	S	S	S	S	P
Medial	S	P	S	P	X	P	X	P
Total P, Florida forms	0	2	0	1	0	1	0	2
Viets, 1927	0	2	0	1	0	1	0	2
Trouessart, 1889	?	2	?	2	?	2	?	2
R. pectinatus	?	2	?	1	?	1	?	1

Carpite long, slender, shaft not moniliform, not visibly fused to end of tarsus. Median claw absent. Lateral claws with an elaborate, fan-shaped (when seen ventrally or dorsally) expansion which bears a row of about 20 long, slender teeth along its distal margin. A second female has a narrower plate with only 10–15 teeth along the distal margin.

Evidence is shown in Fig. 11 that the carpite is attached to the end of the tarsus (or the carpal membrane), despite the fact it does not appear to be joined. All but the basal portion of the carpal membrane had been torn off, which must have occurred prior to mounting, for the claws could not be found in the glycerine mount. In addition, the writer cannot recall any case in which claws have been broken off mites while the legs were being dissected. Furthermore, two of the other posterior tarsi had been broken off near the ends prior to the death of the mite, possibly in an encounter with an amphipod or other predator, for they showed complete healing of the injury. But in the one tarsus drawn, only the ambulacrum had been injured, and despite this injury the carpite remained attached to the tarsus. This is probably the condition in all Rhombognathinae, although the fusion of the carpite to the tarsus is apparent only in *Isobactrus*.

Deutonymph. Dorsal plates as in adult, but of smaller size. OC with setae nearer edge of plate, especially the anterior seta. Three pores and 2 perforate corneae present. Setae of PD at edge of plate. Epimeral plates separated by weakly striated cuticle. Setae arranged as in adult, except for those around genital opening. Genital plate (Fig. 7) with no clearly defined suckers. Two pairs of large setae and a pair of subgenital setae present. Anal plate completely separate from genital plate. Capitulum projecting to a point slightly beyond middle of I-3. Pectinate setae as in adult, but pectinations less distinct. Claws as in adult.

Remarks. Although the size and form of the plates would suggest this form to be identical with *R. pectinatus* Viets 1936, which was taken on Bonaire and Curaçao off the Venezuelan coast, Viets' description of that form as having the capitulum almost completely concealed under the anterior end of the body makes it impossible to relate the two. Since the condition pointed out by Viets would be unique in this genus, it would be desirable to have a more exact description of the orientation of the capitulum. This condition is characteristic of *Isobactrus*, but that group is generically distinct from *Rhombognathus*.

Either there has been too little search for *fundamental* distinguishing characters in some of the closely related forms of this genus, or else there are none, in which case certain names must be abandoned. Probably the only way to obtain a final answer to the question of the validity of the morphological characters in this genus is by rearing isolated females in aquaria under different conditions and analyzing the distribution of these characters in the resulting progeny.

Three females taken at Solomon's Island, Maryland, key out to *R. magnirostris magnirostris* in Viets' key (1939c: 530–534), and agree with the above description in all major details except for the form of the comb on the lateral claws. This is very short in the three specimens and contains only five or six teeth. The arrangement of the pectinate setae on the legs is exactly as given for the Florida specimens. There are no pectinate setae on segment 4 of any of the legs. It should be noted that considerable variation is found in the degree of development of the comb on the lateral claws of the Florida specimens.

Distribution. North America: Florida (Biscayne Bay, on Soldier's Key); Chesapeake Bay (Solomon's Island, Maryland).

French Mediterranean, Adriatic, Black Sea, French Atlantic, English Channel, North Sea (Norway).

Rhombognathus magnirostris var. *lionyx* Trouessart 1900

Trouessart 1900a, 38: *Rhombognathus magnirostris lionyx*, new variety. Trouessart 1901a, 252: *Rhombognathus magnirostris lionyx* Trt. Viets 1927a, 97–98, 100–102, etc.: *Rhombognathus* (s. str.) *magnirostris lionyx* Trt. 1889. Viets 1927b, 8, 11, 47, 53–55: *Rhombognathus* (s. str.) *magnirostris lionyx* Trt. 1889. Schulz 1933, 97, 102: *Rhombognathus magnirostris lionyx* Trt. Viets 1939c, 531, 539: *Rhombognathus magnirostris lionyx* Trt. 1899.

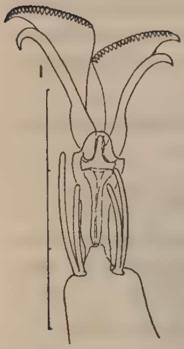
Remarks. This form is known in North America from a single deutonymph from Beaufort, North Carolina. In most features it is very similar to deutonymphs of *R. magnirostris magnirostris*, but the claws are completely smooth. The distribution of pectinate setae on the legs differs slightly from that given by Viets (1927a: 101), but since the validity of this questionable character has never been demonstrated, no new name can be given. The arrangement and form of the setae on segments 4 and 5 is as follows (S = smooth, P = pectinate, X = no seta present in this position):

	I		*II*		*III*		*IV*	
	4	*5*	*4*	*5*	*4*	*5*	*4*	*5*
Ventro-lateral	P	P	S	S	S	P	S	P
Medial	S	P	S	P	X	P	X	P
Total P	1	2	0	1	0	2	0	2
Viets, 1927a	1	2	0	1	0	1	1	2

Viets noted a single pectinate seta on both III-5 and IV-4, but otherwise there is agreement between his specimens from the Baltic and those from Florida.

Distribution. North America: Beaufort, North Carolina (Piver's Island).

Southern Pacific (Macquarie Islands), Adriatic, English Channel, North Sea, Baltic, Arctic Ocean (Spitzbergen).



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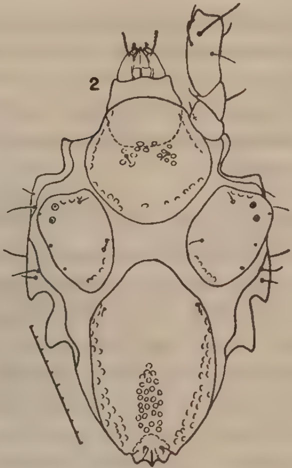

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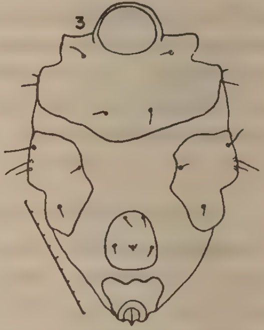

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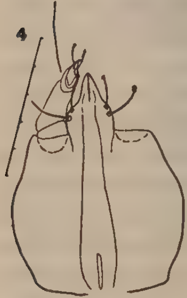

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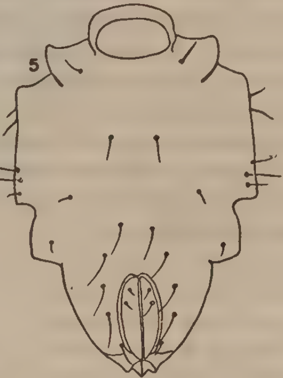

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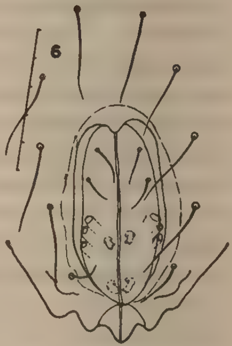

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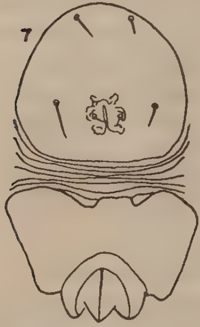

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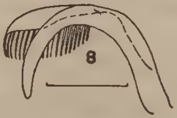

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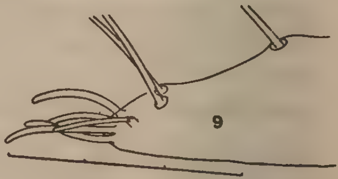

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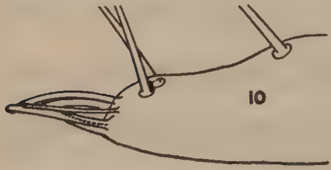

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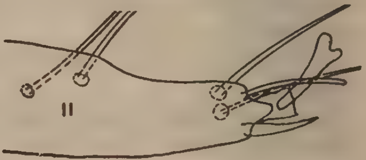

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Genus *Rhombognathides* Viets 1927, emended

Viets 1927a, 88–89, 106: *Rhombognathides*, new subgenus. Viets 1927a, 88–89, 107: *Rhombognathopsis*, new subgenus. Viets 1939c, 528, 533–535: *Rhombognathopsis* Viets. Viets 1939c, 528, 534: *Rhombognathides* Viets.

Diagnosis. Genital opening of female terminal and guarded by a pair of large, cusp-like opercula (the modified genital sclerites). Armor usually heavy in adult. Claws angularly bent and pectinate, or scythe-shaped and with or without accessory tooth. Two claws on all tarsi, or 3 on I-II and 2 on III-IV, or 3 claws on all tarsi. I-6 and II-6 with only the bacillum, which is long and rod-shaped and more than five times as long as thick in forms known to the writer. Genital and anal plates completely fused.

Type. *Rhombognathides pascens* (Lohmann) 1889 (= *Aletes pascens* Lohmann 1889), by original designation.

Remarks. The synonymic status of *Rhombognathopsis* is discussed in detail on pages 26 to 27, and 29.

KEY TO NORTH AMERICAN SPECIES (ALL STAGES)

1a. Lateral claws completely smooth, with neither accessory tooth nor pecten. Ocular plates with single cornea..............*merrimani* new species; p. 56.
  2a. All legs lacking median claw; only lateral claws present.
    merrimani merrimani new species, new variety; p. 56.
    North America (New Brunswick).
  2b. Legs I–II with median claw and lateral claws; III-IV with lateral claws.
    merrimani needleri new species, new variety; p. 59.
    North America (New Brunswick).
1b. Lateral claws pectinate. Ocular plates with single cornea.
  3a. Median claw on all legs ¾ as long as lateral claws. Setae surrounding genital area of male reaching to or beyond middle of GA. A pair of setae in the membranous area between AD and PD.......*mucronatus* Viets 1927; p. 54.
    North Sea, North America.
  3b. Median claw on all legs or only on I and II; only ½ as long as lateral claws. Setae surrounding genital area of male not reaching to middle of GA. All dorsal setae included within the plates.

Figures 1–11. *Rhombognathus magnirostris magnirostris* Trouessart 1889. *1* Female: I-6, ventral view. *2* Female: dorsum. *3* Deutonymph: venter. *4* Deutonymph: venter. *5* Female: venter. *6* Female: genito-anal region. *7* Deutonymph: genito-anal region. *8* Female: IV-6, outer aspect of claw. *9* Female: I-6, lateral view, ambulacrum omitted. *10* Female: II-6, lateral view, ambulacrum omitted (same scale as *9*). *11* Female: III-6, ventro-medial view (same scale as *9*).

4a. Median claw on only legs I and II (except Schulz 1935?). Body 300–360μ long................................*pascens* (Lohmann) 1889; p. 48.
Black Sea, French Atlantic coast, North Sea, Baltic, England, Ireland, North America.

4b. Median claw on all legs. Body 360–420μ long (but usually distinctly longer than *pascens*)..........................*seahami* (Hodge) 1860; p. 51.
Baltic, North Sea, French Atlantic coast, England, Ireland, North America.

Rhombognathides pascens (Lohmann) 1889

Figures 12–19

Lohmann 1889a, 321–330, etc.: *Aletes pascens*, new species. Trouessart 1889a, 229: *Rhombognathus pascens*. Lohmann 1893a, 16–19, 44, etc.: *Rhombognathus pascens*. Trouessart 1894b, 141, 145, 152: *Rhombognathus pascens*. Lohmann 1901a, 281–283: *Rhombognathus pascens*. Viets 1927a, 89, 106, 109, etc.: *Rhombognathides pascens* (Lohm.) 1889. Viets 1927b, 11–13, 63, 66, etc.: *Rhombognathides pascens* (Lohm.). Schulz 1935a, 86–87: *Rhombognathides pascens* s. str. Viets 1939c, 534: *Rhombognathides pascens* var. Schulz 1935. Viets 1940g, 105, 106, 110: *Rhombognathides pascens*.

Female. Body 305–360μ long, 201–235μ wide (av. 326 x 213μ); L/W = 1.45–1.62 (av. 1.53), based on 10 females. AD an elongate, anteriorly rounded pentagon, the panelling usually confined to the median and antero-lateral portions of the plate; 1 pair of setae. OC four-sided, with a single cornea and 3 setae; panelling usually distributed as shown in Fig. 12. PD straight anteriorly, with sloping antero-lateral margins; elliptical posteriorly; 5 pairs of setae; panelling arranged in 3 rows as shown in Fig. 12. Membranous areas greatly reduced, lacking setae; striae distinct, parallel. In a female 325μ long the following measurements were obtained (L/W): AD 105/100; OC 75/63, and 76/63; PD 193/153μ; AD-PD 12μ, OC-OC 65μ. AE (Fig. 13) undivided, with 3 pairs of minute setae. PE with 2 pairs of setae ventrally and 1 pair dorsally. GA undivided. Genital opening

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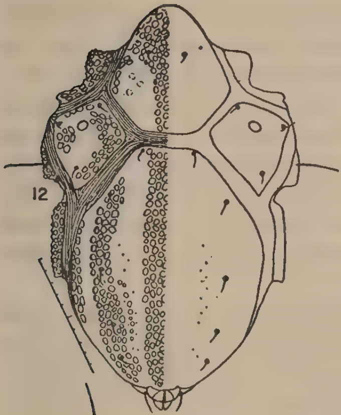
Figures 12–19. *Rhombognathides pascens* (Lohmann) 1889. *12* Female: dorsum. *13* Female: venter. *14* Female: capitulum, ventral view (body 325μ long). *15* Deutonymph: venter. *16* Male: genito-anal area (body 360μ long). *17* Deutonymph: dorsum. *18* Male: lateral leg of claw III (shaft of claw parallel to optical axis of microscope). *19* Male: lateral claw of leg III, ventral view.

Figure 20. *Rhombognathides seahami* (Hodge) 1860. Male: genito-anal area (body 375μ long).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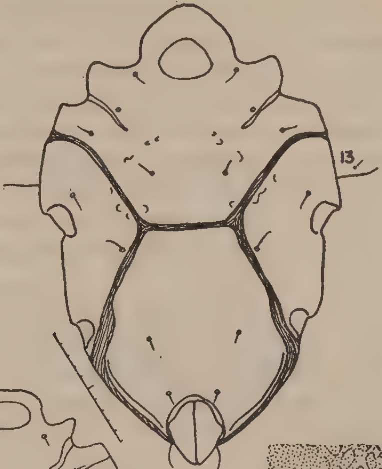
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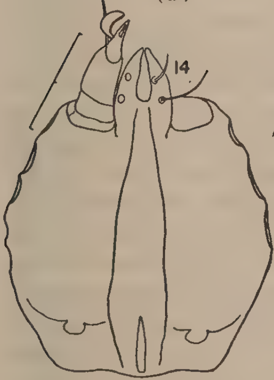
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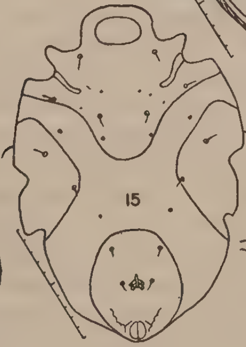
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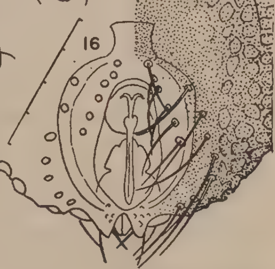
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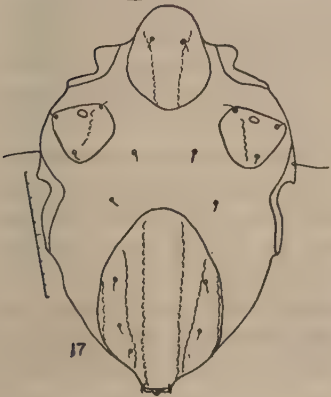
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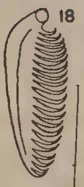
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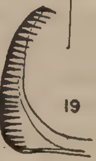
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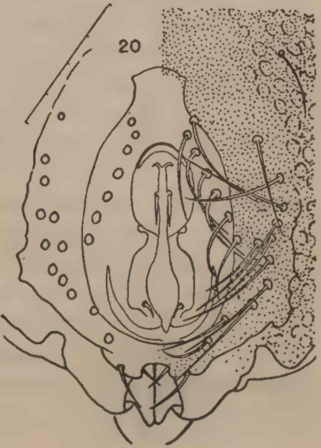
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completely terminal, extending beyond the anal papilla and concealing the latter in ventral view. Three pairs of setae ventrally; 1 pair on anal papilla. Membranous areas greatly restricted, striate.

Capitulum (Fig. 14) rather elongate and panelled dorsally; rostrum somewhat swollen, with 2 pairs of setae ventrally. Palpi with lateral seta on P-4 greatly enlarged, flattened. In a female with a body length of 367μ the following measurements were obtained: capitulum 72μ long to tip of rostrum and 59μ wide; rostrum alone 18μ long and 12μ wide. Legs as in *R. seahami*, except that there is no median claw on III-6 and IV-6.

Male. Body 284–340μ long, 187–229μ wide (av. 314 x 208μ); L/W = 1.47–1.55 (av. 1.51); based on 10 specimens. Those from New Haven are slightly smaller than those from Woods Hole. Male somewhat more rounded posteriorly than female as a rule. Form and panelling of dorsal plates on male and female identical.

Genital area (in a specimen 360μ long) enclosed in an unpanelled, punctate area, about 51μ wide, in each side of which are found 14 to 17 setae. Genital opening immediately surrounded by a flask-shaped area 56μ long and 39μ wide, produced (as in *R. seahami*) by an internal thickening of the cuticle. In some specimens the "neck" of the "flask" is not distinct. Genital area placed relatively further back than in *R. seahami*, so that only the tip and the sides of the anal papilla are visible through the V-shaped apical notch. The differences between the genital areas of *R. pascens* and *R. seahami* seem to be largely associated with this posteriad displacement. Capitulum as in female.

Deutonymph. Easily recognizable by claws. Dorsum and venter as shown in Figs. 17 and 15. PD with anterior 2 pairs of setae lying in the membranous area rather than in PD as in adult. GA undivided; only 2 pairs of setae. Two pairs of genital suckers present; subgenital setae absent. All ventral setae inserted in the plates. Leg IV with 6 segments.

Protonymph. Resembling the deutonymph in general appearance but smaller; a single pair of genital suckers and leg IV with 5 segments. Both nymphs vary in appearance with degree of repletion. Plates not increasing in size between the molts, so that in more mature nymphs the membranous areas are relatively more extensive.

Remarks. This species not only resembles, but is truly related to, *R. seahami* (Hodge). The two species are certainly more closely related to each other than to any other species of Rhombognathinae.

It seems most unreasonable, therefore, to separate them on the basis of the median claw on III and IV, as Viets did. Therefore, *Rhombognathides* Viets 1927 is redefined to include both forms, with *R. pascens* as type.

Distribution. North America: Woods Hole, Massachusetts; New Haven County, Connecticut (Double Beach; Morgan Point).

French Atlantic, English Channel, Ireland, North Sea, Baltic, Black Sea.

Rhombognathides seahami (Hodge) 1860

Figures 20–23

Hodge 1860, 319: *Pachygnathus seahami*, new species. Lohmann 1889a, 274, 322, 325–326, etc.: *Aletes seahami* (Hodge); 326: *Aletes triunguiculatus* (a provisional name). Trouessart 1889a, 229–230: *Rhombognathus seahami*. Viets 1927a, 89, 107, 109, 152–153, 155–164, 166–171: *Rhombognathopsis seahami* (Hodge). Viets 1927b, 12–13, 38, 46–48, 52–55, 65–66: *Rhombognathopsis seahami* (Hodge).

Female. Body 381–416μ long, 242–270μ wide (av. 397 x 260μ); L/W = 1.44–1.62 (av. 1.53); based on 10 females. Noticeably larger than *R. pascens* even macroscopically, but identical in form. Form of dorsal plates, chaetotaxy and sculpturing as in *R. pascens*, so that Fig. 12 (*pascens*) will also serve for the recognition of this species. Ventral surface also as in *R. pascens*. Capitulum identical with that of *R. pascens*, but larger. In a female with a body length of 395μ the following measurements were obtained: capitulum 76μ long to tip of rostrum and 63μ wide. Rostrum alone 19μ long and 14μ wide. Palpi as in *R. pascens*. Legs rough, panelled; femora I and II swollen, the ratio of dorsal length to maximum height about 1.31 and 1.43 respectively. Femora III and IV swollen, about 1.57 and 1.62 times as long as high respectively. Setae as follows (*d.* = dorsal, *l.* = lateral, *m.* = medial, *v.* = ventral):

	I				*II*				*III*				*IV*			
	d.	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*
1.	–	–	–	1	–	–	–	1	–	–	1	–	–	–	–	–
2.	1	1	–	–	1	2	–	–	1	–	1	–	1	1	–	–
3.	3	1	–	–	1	1	2	–	2	1	–	–	2	1	–	–
4.	1	1	1	–	1	1	1	–	1	1	–	–	2	1	–	–
5.	3	2	–	–	3	2	–	–	3	2	–	–	3	2	–	–
6.	3	1	–	–	3	1	–	–	4	–	–	–	3	–	–	–

I-3 with a finely serrate seta dorsally. I-5 with a pair of broad, very finely pectinate setae ventrally. I-6 like II-6. II-5 with only the medial member of the ventral pair pectinate, the other slender and tapering. II-6 (Fig. 21) with a single dorsal seta near middle and a pair of dorsal setae nearer the end of the segment. Just anterior to the lateral member of this pair is a long bacillum. Parambulacral setae divaricate. Ventro-medial seta of III-5 and IV-5 rather heavy and usually faintly pectinate. III-6 with dorsal seta near middle of segment duplicated; IV-6 with the usual single seta here. Bacillum lacking. Parambulacral setae of III-6 divaricate medially; ventral member heavy, spine-like and the dorsal member long, slender, rod-like; only a single spine-like seta present laterally. On IV-6 only a pair of heavy, spine-like setae is present. (See also the discussion of the parambulacral setae of *Metarhombognathus armatus americanus*, n. subsp.). Two lateral claws and median claw on all legs (Figs. 21, 22, 23).

In a female with a body length of 416μ the following measurements were obtained:

	1+2	*3*	*4*	*5*	*6*	*Ambul.*	*Total*	*T/BL*
I	51μ	71	30	55	55	30	292	.70
II	50	66	30	53	55	33	287	.69
III	65	55	28	53	58	40	299	.72
IV	71	56	30	50	61	38	306	.74

Male. Body 360–395μ long, 242–270μ wide (av. 371 x 261μ); L/W = 1.36–1.58 (av. 1.48); based on 10 males. Appreciably larger than male of *R. pascens*. More rounded posteriorly than female.

Genital area as shown in Fig. 20, consisting of an area of punctate cuticle 75μ wide (specimen 375μ long) in which genital opening is found surrounded by 19 to 22 setae on each side. Genital opening immediately surrounded by a flask-shaped area 77μ long and 43μ wide, apparently produced by an internal thickening of the body wall. Genital area distinctly elevated from anal area posteriorly, with a rectangular apical notch, leaving anal papilla almost completely exposed. In the latter two features, *R. seahami* appears to differ quite

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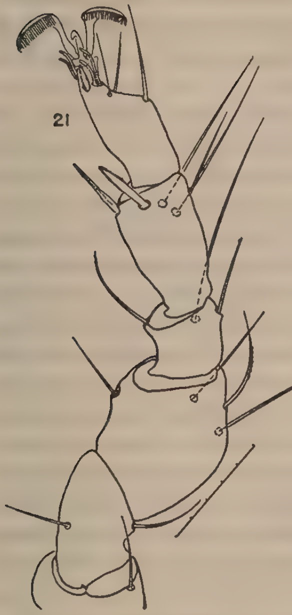
Figures 21–23. *Rhombognathides seahami* (continued). *21* Female: leg I, median view. *22* Male: II-6, lateral view. *23* Male: I-6, ventro-lateral view.

Figures 24–26. *Rhombognathides mucronatus* (Viets) 1927. *24* Protonymph: genito-anal plate. *25* Male: ambulacrum of leg IV, disti-ventral view. *26* Male: genito-anal area.

Figure 27. *Rhombognathides merrimani merrimani* new species, new variety. Male: genito-anal area.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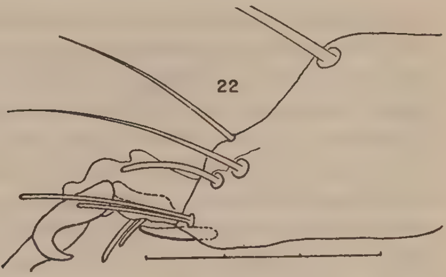
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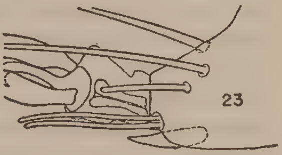
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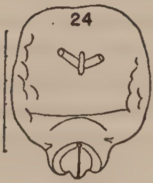
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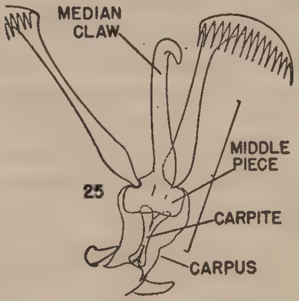
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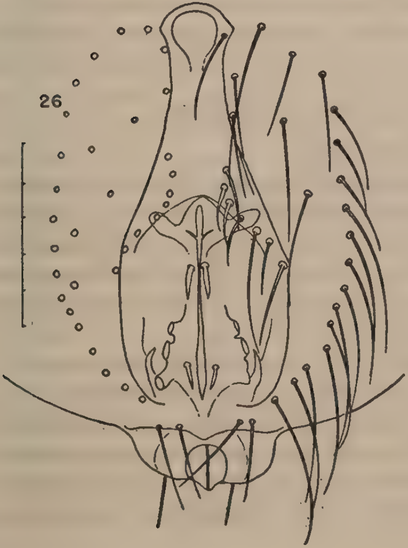
CARPUS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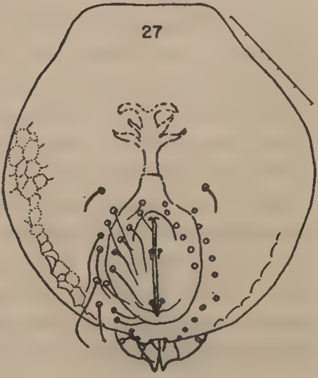
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consistently from *R. pascens.* One *R. seahami* male was found in which the genital area is displaced far posteriorly as in *R. pascens*, but the apical notch is rectangular (not V-shaped) and it is otherwise clearly recognizable as a male of *R. seahami.*

Remarks. A comparison of figs. 22 and 28 in Viets (1927b: 11, 13) would indicate an appreciable difference in the relative extent of the membranous areas and plates in *R. pascens* and *R. seahami. R. seahami* (female dorsum) is shown as having relatively wide spaces between the plates, such as one would find in a deutonymph (although it is obvious that Viets' figure was not drawn from a deutonymph, as indicated by the positions of the dorsal setae), or in an extremely replete female. Lohmann (1889a: figs. 64, 88) showed no such difference in the extent of the membranous areas. Lohmann's fig. 88 (dorsum of *R. seahami*) was drawn from a male, but Lohmann did not state which sex of *R. pascens* he illustrated by his fig. 64; since he had both males and females of this species, no assumption would be safe. But his figs. 64 and 88 could very well represent the same species, showing that Lohmann's specimens of *R. pascens* and *R. seahami* were as similar in dorsal view as those seen by the writer in North America. As pointed out above, a drawing of either species in dorsa view could serve for the other as well.

Distribution. North America: Woods Hole, Massachusetts.

French Atlantic, English Channel, Ireland, North Sea, Shetland Islands, Baltic.

Rhombognathides mucronatus (Viets) 1927

Figures 24–26

Viets 1927a, 107, 113–115, 153–156, 158–164, 170–171: *Rhombognathopsis mucronatus*, new species. Viets 1927b, 12, 14–15, 52–55: *Rhombognathopsis mucronatus* Viets. André 1939b, 239: *Rhombognathus mucronatus* Viets. Viets 1939c, 534–535: *Rhombognathus* (*Rhombognathopsis*) *mucronatus* Viets 1927. Viets 1940g, 110: *Rhombognathopsis mucronatus* Viets.

The writer has taken this species from three localities and has only two males and a few nymphs. It is easily identified, however. Its claws, the weakly developed panelling and the presence of one of the pairs of dorsal setae in the membranous area provide sharply defined diagnostic characters to differentiate it from *R. pascens* and *R. seahami*, to which it is most closely related. Viets (1927a: 114) figured the female dorsum, the male GA, chelicera, palp, and tarsi I to IV, as well as (1927b: 15) the male dorsum and male and female venters.

Adult. Body 430μ long (Viets: 450μ). Dorsal plates somewhat less extensive than in *R. pascens*, with a pair of setae in the membranous area between AD and PD. The homologues in *R. pascens* and *R. seahami* are included in PD. OC each with 3 setae and 2 corneae, the posterior cornea extremely rudimentary and possibly occasionally absent. Dorsal plates with panelling weakly developed as a rule, finely and densely porose. Female with membranous areas more extensive (at least in gravid females) than in male; AD and PD separated by a distance as great as, or greater than, length of OC. Male, and perhaps young females, with AD and PD separated by a distance less than length of OC.

Ventral plates finely and densely porose, but panelling invisible at low magnifications (150x), and only faintly visible along sides of plates at higher powers (645x). In *R. pascens* and *seahami* the panelling is readily visible even at 50x. Female with genital opening terminal, guarded by cusp-like opercula (Viets 1927b: 15). Male GA with flask-shaped area greatly elongate, extending well beyond middle of plate and surrounded by from 30 to 35 slender setae. Apical notch not developed. Three pairs of genital suckers (Fig. 26).

Chaetotaxy of legs as in *R. seahami.* Ventral seta of I-4 faintly pectinate. Both ventral setae on III-5 may be pectinate rather than just the medial one. Otherwise the pectinate setae are as described for *R. seahami.* Bacillum, prebacillum and parambulacral setae of all legs morphologically identical with those of *R. seahami, pascens* and *merrimani.* Carpite typical for the genus. All legs with a pair of angularly bent, pectinate claws, and with a median scythe-shaped claw at least ¾ as long as lateral claws (Fig. 25).

Deutonymph. Easily recognizable by claw characters. OC with 3 setae and 2 corneae as in adult. Two pairs of setae between AD and PD as in nymphs of *R. seahami, pascens* and *merrimani.* All legs with 6 segments. GA undivided, with 2 pairs of genital suckers.

Protonymph. Also recognizable by claw characters. OC with 3 setae and a single cornea. Leg IV lacking basifemur. GA undivided, 1 pair of genital suckers. Nymphal plates not showing an increase in size except at time of molt.

Remarks. The position and form of the female genital opening, the form of the male genital area, the chaetography of tarsi I and II, the presence of an undivided GA in both nymphal instars, and the nonisometric growth of the plates in relation to the growth of the body of the nymphs show beyond doubt that *R. pascens, seahami, merrimani,* n. sp., and *mucronatus* form a natural genus. All the characters listed are common to all these species and contrary to those found in *Metarhombognathus,* n. gen. Therefore, *R. mucronatus* and *R. seahami* must not be separated from the other species on the single superficial character of the median claw on all legs; nor can they be allied with such forms as *Metarhombognathus armatus* from which they differ in many fundamental details.

Distribution. North America: St. Andrews, New Brunswick. New Haven County, Connecticut (Double Beach; Morris Cove).

North Sea.

Rhombognathides merrimani, new species

Figures 27–35

This species is represented by two distinct varieties differing principally in the number of claws. *R. merrimani* var. *merrimani* has two claws on all legs. *R. merrimani* var. *needleri* has three claws on I and II, but only two on III and IV. In the author's collection, there are more of the 3–3–2–2 variety than of the 2–2–2–2 variety.

Rhombognathides merrimani, new species, *merrimani,* new variety

Female. Body 319–346μ long, 194–215μ wide; L/W = 1.56–1.70; based on 4 specimens. In a specimen 322μ long the following measurements were obtained (L/W): AD 100/80, OC 75/63 and 76/66, PD 203/136; AD-PD 10μ, OC-OC 58μ.

AD slightly conical anteriorly; capitulum projecting somewhat so that the palpi and a portion of the base are clearly visible from above. AD rounded posteriorly, with a pair of setae just anterior to the middle. OC four-cornered, the margins nearly straight; single cornea present. Three setae and a pore present as shown in Fig. 28. PD extending to middle of OC; anterior margin straight; antero-lateral margins straight or slightly concave; posterior half of PD elliptical, not concealing the anus; 5 pairs of setae. All dorsal plates densely punctate, the panelling feebly developed and distributed as shown in Fig. 28. PD with a central panelled area which is 4 panels wide; lateral areas 2 to 3 panels wide. Membranous areas greatly reduced; striae feebly developed or absent. The inclusion of all the dorsal setae within the dorsal plates emphasizes the relative extensiveness of the plates. Epimera I and II (Fig. 34) completely fused medially. AE usually (but not always) somewhat more rounded posteriorly than in male; PE with 2 pairs of setae ventrally and 1 pair dorsally. GA nearly straight anteriorly. Genital opening extending to end of body, covered by a pair of opercula, the posterior ends of which are directly ventral to the tip of the anal papilla. GA with 3 pairs of setae. All ventral plates densely porose; panelling feebly developed, and sometimes absent on AE.

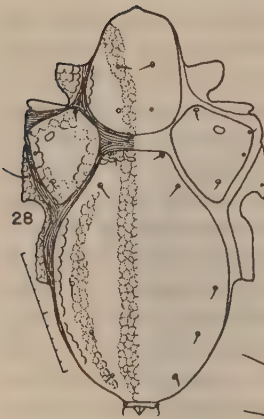
Male. Body 312–325μ long, 201–211μ wide, L/W = 1.48–1.58; based on 3 specimens. Dorsum as described for female. Opposing margins of AE and GA usually straighter (less convex) than in female. GA with 19 to 22 setae on each side as shown in Fig. 27. Cuticle densely porose, panelling indistinct and limited to margin of posterior half of the shield as a rule. Genital opening further anterior than in female and guarded by 2 pairs of setae.

Capitulum (in a male 321μ long) 64μ long; rostrum 19.5μ long and 10μ wide, bearing the usual 2 pairs of setae. Base of capitulum 57μ wide, globular in form, strongly sculptured dorsally, heavily punctate ventrally. Palpi extending beyond tip of rostrum. The drawing (Fig. 35) was made from a specimen in which the ventral margin is inclined ventrad at an angle of about 18°. In other specimens the capitulum appears to be somewhat more conical, probably because it is more nearly horizontal.

Legs with setae as follows (*d.* = dorsal, *v.* = ventral, *l.* = lateral, *m.* = medial):

	I				*II*				*III*				*IV*			
	d.	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*
1.	–	–	–	1	–	–	–	1	–	–	1	–	–	–	–	–
2.	1	1	–	–	1	1	1	–	1	–	1	–	1	–	1	–
3.	3	1	–	–	2	1	1	–	2	–	–	–	2	–	–	–
4.	2	1	–	–	2	1	–	–	1	1	–	–	2	1	–	–
5.	3	2	–	–	3	2	–	–	3	2	–	–	3	2	–	–
6.	3	1	–	–	3	1	–	–	4	–	–	–	3	–	–	–

I-1 with very fine medial seta; I-5 with ventral setae flattened and pectinate like medial seta on II-5. I-6 with 3 setae dorsally in addition to the long bacillum at base of ambulacrum. Parambulacral setae divaricate; a single spine ventral to base of ambulacrum. II-5 with only the medial member of ventral pair pectinate. II-6 resembling I-6. Tarsi I and II with a median claw which is of the same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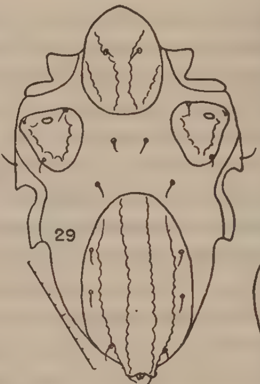
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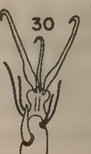
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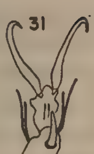
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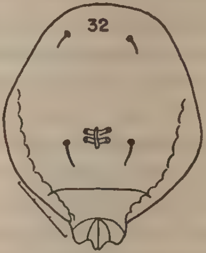
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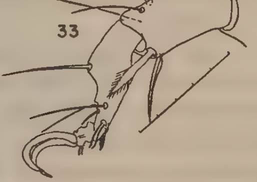
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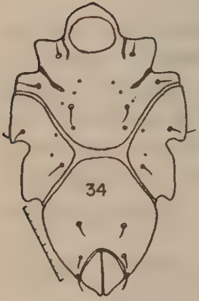
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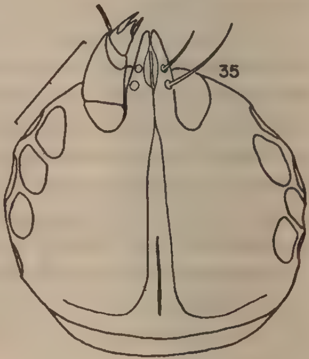
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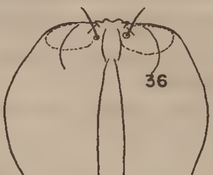
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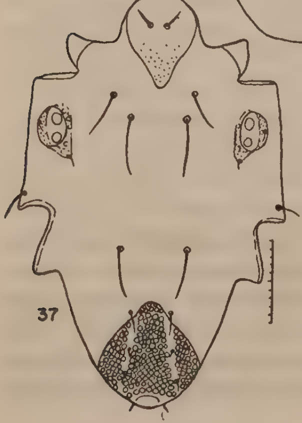
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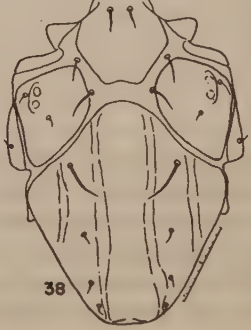
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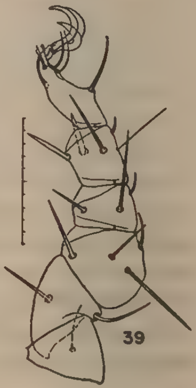
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form as lateral claws but somewhat smaller; lateral claws completely smooth (Fig. 30). III-5 with medial member of ventral pair pectinate, as on II-5; the other one very minute, simple. III-6 with 2 pairs of setae dorsally. Claws slender, scythe-shaped, without comb or accessory tooth. Lengths of leg segments as given below for *R. m. needleri.* Parambulacral setae identical morphologically with those of *R. seahami*, *mucronatus* and *pascens*, and also *Metarhombognathus armatus americanus.*

Deutonymph. Easily recognizable by claw characters and sculpturing. Dorsal plates (Fig. 29) less extensive than in adult; PD with only the 3 posterior pairs of setae; the 2 anterior pairs in the membranous area. GA with only 2 pairs of setae and 2 pairs of suckers; subgenital setae absent. Genital and anal portions separated by a delicate transverse line which does not appear to divide the plate. In young deutonymph, all plates are very close together, as in adult.

Protonymph. Also easily recognized by claws and plates. Leg IV with only 5 segments.

Rhombognathides merrimani, new species, *needleri*, new variety

This variety is identical with *R. m. merrimani*, n. sp., n. var., in all respects except the claws and cuticular characters, so that Figs. 27 to 35 suffice for this variety also. The cuticle of *R. m. merrimani* appears to be slightly darker (perhaps thicker) and the punctations and panelling are slightly more distinct.

Chaetotaxy of legs as described for *R. m. merrimani.* Legs III and IV longer than I and II. In a female with a body length of 332μ the following leg measurements were obtained (dorsal length in μ).

	1+2	*3*	*4*	*5*	*6*	*Ambul.*	*Total*	*T/BL*
I	35μ	68	23	51	37	35	249	.75
II	32	61	23	50	45	33	244	.74
III	53	50	22	45	56	37	263	.79
IV	50	51	23	51	56	35	266	.80

Figures 28–30. *Rhombognathides merrimani merrimani* (continued) *28* Female: dorsum (slightly rotated). *29* Deutonymph: dorsum. *30* Male: I-6, ventral view.

Figure 31. *Rhombognathides merrimani needleri* new species, new variety. Male: I-6, ventral view.

Figures 32–35. *Rhombognathides merrimani merrimani* (continued). *32* Deutonymph: genito-anal plate. *33* Male: leg II, median view. *34* Female: venter. *35* Male: capitulum, ventral view.

Figures 36–39. *Metarhombognathus armatus americanus* new subspecies. *36* Male: capitulum, ventral view. *37* Male: dorsum. *38* Deutonymph: dorsum (specimen from St. Andrews, New Brunswick). *39* Female: leg I, lateral view.

Remarks. This species is closely related to *Rhombognathides trionyx* (Trouessart) as described by André (1939c: 310–312). The principal differences are the possession by *R. merrimani* of a single cornea instead of two; and the large setae on I-5 of *R. trionyx* are smooth and not feathered. Certain differences in the chaetotaxy of the ventral plates may also exist, judging from André's illustration, but this is not certain.

Distribution. Both varieties have the same type locality: St. Andrews, New Brunswick. They have not been taken elsewhere.

Genus *Metarhombognathus*, new genus

Diagnosis. Three very heavy scythe-shaped claws (in forms known at present) on all tarsi; median claw nearly as heavy as lateral claws. Genital opening of female subterminal and not guarded by cusp-like opercula. I-6 with bacillum and prebacillum; II-6 with bacillum only; these are short and club-shaped and less than five times as long as thick. Deutonymphs more heavily armored than adults. Epimeral plates greatly reduced in adult but normal in deutonymph. Genital and anal plates of protonymph and deutonymph undivided but those of adult separated by band of striate cuticle.

Type. Metarhombognathus armatus (Lohmann) 1893 (= *Rhombognathus armatus* Lohmann 1893).

Remarks. Only one North American form is known, *Metarhombognathus armatus americanus*, new subspecies.

Metarhombognathus armatus armatus (Lohmann) 1893

Lohmann (1893a: 18) described this form briefly in a footnote, but the description was incomplete because Lohmann had only deutonymphs (although on page 42 he noted that he found a mature individual in August). A free translation of the principal points in Lohmann's description is as follows:

> Most noteworthy are (1) the claw structure: middle piece of claw drawn out into a long slender claw nearly like the lateral claws; and (2) the characteristic structure of the dorsal plates: closely spaced, nearly circular panels with somewhat elevated, wall-like margins. Large genito-anal plate present. Capitulum 80μ long, body 300μ long ventrally; total length 380μ. Form of body plump, legs very heavy, posterior end broadly rounded.

Trouessart (1901c: 152) said (author's translation):

I have taken the adult at St. Guenole. The species is well characterized by the slender triple claws on all legs, the middle claw being as well developed as the lateral ones. In the adult the armor is very heavy, the plates joining completely and bearing sculpturing resembling that of the subgenus *Copidognathus*. Segment 4 of legs I and II is strongly swollen above. Total length 500μ.

Viets (1927a: 108–111) described carefully the deutonymph of *Rhombognathopsis armatus*, based on material from Helgoland, and also described as new *Rhombognathopsis mollis*, based on males and females taken at the same places where *armatus* was found. The chief differences between *armatus* Lohmann and *mollis* Viets 1927 are in the degree of development of the armor, which in *armatus* is heavy, extensive, and deeply sculptured and in *mollis* greatly reduced and without sculpturing except on the minute post-dorsal plate. The dorsal plates of *mollis* are greatly reduced and the ocular plates are virtually absent. Because of these differences, Viets considered these two forms (one known only from the deutonymph, the other from the adult) as separate species.

However, observations of the author show that *mollis* is identical with *armatus*. These observations have been made on a form which is beyond any doubt a subspecies of *armatus* Lohmann and which is similar to the latter in virtually all respects except the degree of development of the deutonymphal armor. The adults are very weakly armored as in *mollis* Viets. Conclusive evidence of the relationship between these two instars was obtained by dissecting an adult from a quiescent deutonymph (Slide 43-177-75b). Even before this, however, convincing circumstantial evidence of the identity of the two was obtained. Both the deutonymph and adult are very common on the Connecticut coast; these are the only two forms with three heavy, smooth, scythe-shaped claws. Considering the extent of the collections made, it is virtually impossible that two such abundant forms could coexist with one being known only as the deutonymph and the other only as the adult. The two forms displace each other seasonally, the heavily armored nymphs appearing from May to December and the adults from December to June. Viets (1927a: 160) recorded "*mollis*" only in spring collections and *armatus* only in summer collections, which corresponds exactly with the situation in the North American subspecies. Also, many adults are found which have traces of the heavy nymphal panelling on the ocular plates. Although the writer has never seen specimens of the European form, there is no doubt that the situation in the European subspecies is identical with that in the American subspecies. Therefore: *Metarhombognathus armatus* (Lohmann) 1893 (= *Rhombognathus armatus* Lohmann, = *Rhombognathopsis mollis* Viets 1927).

The only question remaining is, why did Trouessart report the adult of *armatus* Lohmann as being heavily armored, with the plates joining completely? It seems possible that the very weakness of the plates, rendering their limits indistinct, caused Trouessart to consider the dorsal plates as continuous; but there is no three-clawed halacarid yet known in which the latter condition exists. It is also possible, of course, that Trouessart had another species.

As Viets pointed out, a reduction in the armor plates at the molt would be unique in a halacarid; therefore one can appreciate Viets' reluctance to accept the adults of this species as being derived from the heavily armored deutonymphs which Lohmann called *armatus*. It is ironic that the most weakly armored of all Rhombognathinae should be named *armatus*.

Distribution. North Sea; French Atlantic (?).

Remarks. *M. nudus* (Viets) 1928 and *Rhombognathopsis contectus* Viets 1928 provide a case parallel to that of the above two subspecies. These were taken at the same place (Murmansk coast, Kolafjord, at the north end of Olenij Island, on *Diploderma*, July 19, 1924). Considering the close similarity between the weakly armored *M. nudus* and adults of *M. armatus*, and between the heavily armored *R. contectus* and deutonymphs of *M. armatus*, there is no doubt that *contectus* is a synonym of *nudus* (which was named and described first). Here again, without direct evidence, there is the very strong suggestion from the abundance of the two forms that they are adult and deutonymph of the same species. Viets (1928g: 83) described both as "zahlreich." It is highly improbable that two extremely closely related forms (as shown by the unique structure of the lateral claws) could occupy the same habitat, both forms being numerous, and yet one be known only as the adult and the other only as the deutonymph. But the most convincing evidence is the obvious close phylogenetic relationship between *M. nudus* and *M. armatus americanus*, n. subsp., in the latter of which the conspecificity of the adult and deutonymph has been conclusively demonstrated.

Metarhombognathus armatus americanus, new subspecies

Figures 36–53

Male. Body 350–450μ long. Similar to *M. armatus armatus* Lohmann in most respects, but somewhat smaller. In one male 405μ long and 285μ wide the following measurements were obtained (L/W): AD 100/80, OC 52/45, PD 103/93μ. AD pyriform, with panelling only on small posterior portion; 2 heavy setae present. OC reduced to a small oval area containing 2 corneae and surrounded by a punctate area which may include a few shallow panels. One small seta lateral to corneae and 1 at posterior end of plate. PD faintly panelled except on the 2 longitudinal costae; 3 pairs of setae included in the plate. AE with right and left sides separated by a wide interval as in *M. armatus armatus.* GA very feebly developed but large, consisting of a broad elliptical area in which striations are lacking; chaetotaxy only slightly different from that of the European form as figured by Viets. Chelicera 93μ long, apparently somewhat more curved than in the European form, and with a more slender claw 22μ long. Palpi and legs as in female.

Female. Somewhat larger than male, at least in spring when the abdomen is filled with eggs; 350–550μ long. Dorsal plates comparable in form and size to those of male. In a specimen 415μ long the following measurements were obtained (L/W): AD 100/75, OC 50/42, PD 98/93μ.

Ventral surface as in *M. armatus armatus.* Distinct plates lacking in genital and anal areas, but striae completely absent from these portions. Genital and anal portions separated by a narrow band in which striae run transversely. The enclosed areas are neither panelled nor punctate. A single pair of setae lies antero-laterally in genital area; 2 pairs in anal area.

Chelicerae as in male. Capitulum 71–75μ long and 75–79μ wide. Rostrum virtually absent, represented only by a short, truncate cone which is excavated at the tip. A pair of small setae at base of cone and a pair of minute, spine-like processes near tip. Pharynx long, narrow; pharyngeal plate without panels. Palpi 45μ long. P-2 30μ long and 16μ high. P-3 and P-4 fused, forming a 3-segmented palp. P-2 with a long dorsal seta slightly beyond middle. Terminal segment with heavy seta projecting ventro-laterally. Terminal structures difficult to interpret except in a favorable terminal view (Fig. 50) in which a dorso-median seta and 2 heavy lamellar structures can be discerned as in *Rhombognathides* (Viets) 1927. The outer lamella extends very slightly beyond the slender tip of the palp; the inner lamella does not reach to the tip. Chaetotaxy of legs as follows:

	I				*II*				*III*				*IV*			
	d.	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*
1.	–	–	–	1	–	–	–	1	–	–	1	–	–	–	–	–
2.	1	1	–	–	1	1	1	–	1	1	–	–	1	1	–	–
3.	2	1	1	–	2	1	1	–	2	1	–	–	2	1	–	–
4.	2	1	–	–	1	1	1	–	2	1	–	–	2	1	–	–
5.	3	2	–	–	2	2	1	–	2	2	1	–	2	2	1	–
6.	3	1	–	–	3	1	–	–	4	–	–	–	3	–	–	–

In one female (of unknown body length) the following measurements were obtained:

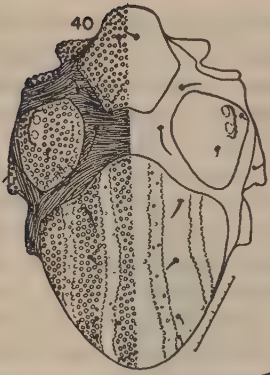
	1+2	*3*	*4*	*5*	*6*	*Ambul.*	*Total*
I	61μ	69/71	39	54	71	50	344
II	62	69/65	41	53	75	53	353
III	89	62/53	36	55	81	59	382
IV	94	66/55	38	57	83	63	401

Trochanter and femur of all legs hirsute, especially dorsally; femur greatly swollen. Femora I-IV 0.97 (higher than long), 1.06, 1.17 and 1.20 times as long as high. All tibiae with 3 setae dorsally, one of which is very slender, and with a very heavy seta ventrally and another ventro-medially; the latter sometimes faintly pectinate (oil immersion). Ventral setae of III-5 and IV-5 completely ventral, not as heavy as those on I-5 and II-5 and apparently always smooth. I-6 and II-6 with 3 setae dorsally and a heavy ventral seta closely applied to distiventral margin of tarsus. Tarsi with claw fossa. Claws scythe-shaped and without accessory tooth. Under oil immersion a roughened ridge can be seen along the outer side of the lateral claws near the convex margin; this appears to represent a crude comb. Median claw scythe-shaped, nearly as large as lateral claws and completely smooth. At the base of the median claw is a thin keel (Figs. 45, 46), which is somewhat larger on leg IV than on leg I.

Deutonymph. 320μ long just after emergence from protonymphal exuvium, but attaining a length of 440μ or slightly greater. Adults upon emergence noticeably smaller than deutonymphs. The general appearance of the nymph does not change during this instar despite the considerable increase in length, for growth of the various parts of the body, at least the legs and plates, is isometric. Dorsal plates very extensive, heavily panelled and thick; panels not angular, but consisting of deep circular pits. AD roughly hexagonal, distinctly concave posteriorly and bearing the usual pair of setae. OC five-sided; 2 corneae on each plate. The usual setae are present, but whereas in the protonymph (and occasionally in the adult) the post-ocular seta is in the membranous area just behind OC, in the deutonymph it is near the center of the plate. PD with 4 heavy longitudinal ridges in which panelling is lacking. Four pairs of setae included in plate, the 2 anterior pairs of which are found in the membranous area in both protonymph and adult. Posterior end of plate distinctly excavated and flattened, projecting beyond end of the body in such a way as to conceal the setae which are readily visible at end of abdomen in adult. Dorsal membranous areas greatly reduced and heavily striate, even in old deutonypmhs. Owing to encroachment of the dorsal plates, only 2 pairs of setae are found here. In a specimen with a body 415μ long and 275μ wide the following measurements were obtained (L/W): AD 113/108, OC 118/93, and 108/85, PD 290/235, AE 98, GA 148/86μ.

Ventral surface also with plates more extensive than in *M. armatus armatus*. AE with right and left halves fused, not divided as in protonymph and adult. Lateral portions of PD visible ventrally. GA well developed and undivided, with 2 internal suckers present. Setae as in *M. armatus armatus;* subgenital setae absent. Panelling usually limited to lateral portions of PE and GA. Legs heavy, as in adult, but claws shorter, relatively heavier, the median claw lacking small keel at base. Chaetography of legs identical with adult in all respects except that IV-2 lacks the dorsal seta and IV-3 lacks the ventral seta. Parambulacral seta of III-6 divaricate laterally but reduced to a single member medially.

Protonymph. Body 270–320μ long; about 0.8 as broad as long. Dorsal plates greatly reduced as in adult. OC variable in shape, usually rounded; single cornea present. Dorsal setae as in adult. Ventral plates greatly reduced; AE divided into right and left halves; a single pair of genital suckers. Panelling developed only on dorsal plates, of same type found in adult. Tarsi with 3 simple claws. Chaetography of tarsi identical with that in adult.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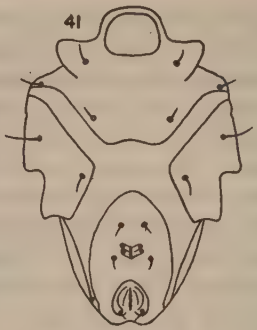
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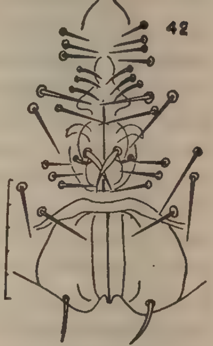
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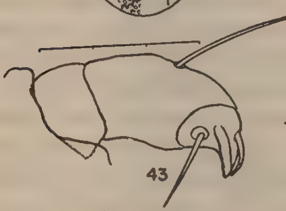
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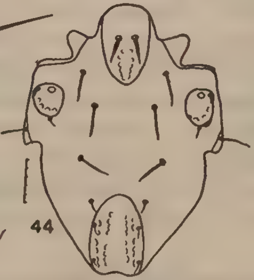
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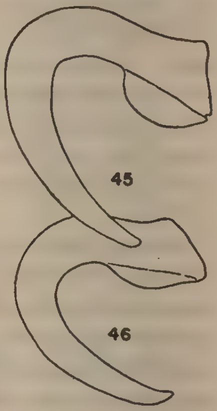
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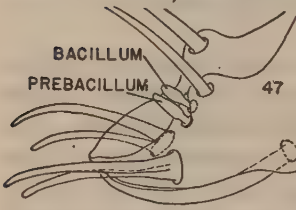
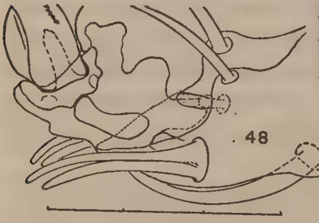

BACILLUM
PREBACILLUM
47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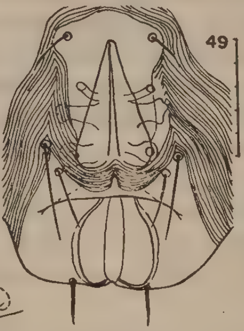
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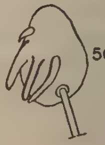
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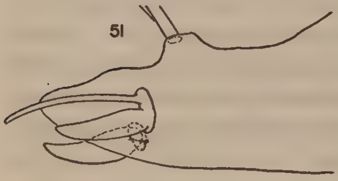
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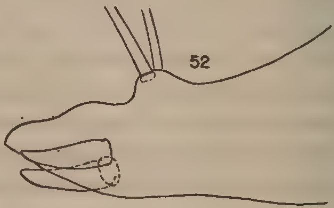
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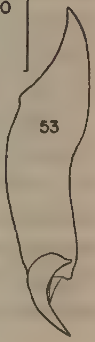
53

Remarks. This subspecies differs from *M. armatus armatus* Lohmann chiefly in the extent of the plates. The plates of the deutonymph are considerably more extensive than is the case in *M. armatus armatus.* In the latter, PD extends just to the level of the dorsal seta of PE, whereas in *M. armatus americanus* PD extends appreciably beyond this point. According to Viets' fig. 28 (1927a: 109), the seta lateral to the corneae lies outside OC, whereas in *M. armatus americanus* it has been found invariably within OC. The medial margin of OC in *M. armatus armatus* is nearly straight, not quite reaching to the line which could be drawn between the anterior seta of the membranous area and the anterior seta of PD; in the new subspecies, OC always exceeds this line and is convex medially. This difference is not associated with the degree of repletion of the nymph, as is the case in all *Rhombognathides* and *Rhombognathus* species, for as pointed out above, the growth of the plates is isometric with respect to the body as a whole. Therefore, young deutonymphs are not relatively more heavily armored than deutonymphs which are quiescent just prior to the final molt. This is unique in the Halacaridae.

The chaetotaxy of the tarsus of this subspecies is of great interest in the morphology of the tarsus of Halacaridae. On I-6 (Fig. 47), just anterior to the lateral member of the disti-dorsal pair of setae, are two setae of slightly different form. The more proximal one (bacillum) is 4.0 to 4.5μ long and has a stalk about half as long as the swollen outer portion of the seta. This is certainly homologous with the bacilliform seta which occupies a corresponding position in other Halacaridae [e. g., *Rhombognathides seahami* (Fig. 22) and *Copidognathus* (s. str.) *punctatissimus* (Fig. 207)]. Anterior to the bacillum is a seta with a relatively shorter stalk, 6.0 to 6.5μ long (prebacillum). The prebacillum is lacking on II-6 and both setae are absent from III and IV. This subspecies also provides convincing evidence of the true homology existing between the parambulacral setae of all the legs. On legs I and II these are divaricate; that is, they consist of a dorsal and a ventral member arising from a single opening in the wall of the

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Figures 40–53. *Metarhombognathus armatus americanus* (continued). *40* Deutonymph: dorsum (specimen from Beaufort, North Carolina). *41* Deutonymph: venter (same scale as *38, 40*). *42* Male: genito-anal region. *43* Female: palp, lateral view. *44* Protonymph: dorsum. *45* Female: median claw IV. *46* Female: median claw I. *47* Female: I-6, lateral view, carpus omitted (same scale as *48*). *48* Female: I-6, lateral view. *49* Female: genito-anal area. *50* Male: left palp, terminal view. *51* Female: III-6, median view (same scale as *48*). *52* Female: IV-6, median view. *53* Chelicera (drawn from a microtome section).

tarsus. On III-6, however, a perfect transition between the divaricate and single-membered condition is found (Fig. 51). The medial parambulacral seta is divaricate, comprising a dorsal setiform member and a ventral spiniform member. Therefore, the spiniform seta is homologous with the ventral seta of I and II. The lateral parambulacral seta consists of a single spiniform seta, indicating that it is the dorsal member which has not developed. The form and position of the parambulacral setae on IV-6 appear to show conclusively that only the ventral member develops. The parambulacral setae in *Rhombognathides pascens, seahami* and *merrimani* are identical, morphologically, with those of *Metarhombognathus armatus americanus.*

Deutonymphs of *M. armatus americanus* were found in abundance at Beaufort, N. C., in October 1944. The Beaufort specimens were identical with the northern form except that the membranous areas were somewhat more extensive. Fig. 40 shows a deutonymph in which the membranous areas were the most extensive of the eight specimens closely studied. In the others the separation of the plates is even less marked. The size of the plates is essentially the same in the two figures, and the anterior setae of PD are the same distance from the edge of the plate. The eight specimens are 374–422μ long, averaging 398.6μ, so that the range of size is probably the same as in the Connecticut deutonymphs (320–440μ).

Distribution. North America: St. Andrews, New Brunswick; New Haven County, Connecticut (West River [type locality], Morris Cove, Pine Orchard); Beaufort, North Carolina (Piver's Island).

Genus *Isobactrus,* new genus

Diagnosis. Genital opening of female ventral in position, not guarded by a pair of large, cusp-like opercula and surrounded by only 3 pairs of setae. Adults more heavily armored than nymphs; all dorsal and ventral plates separate. Ventral plates greatly reduced and not forming a solid shield. Femur I greatly swollen, less than 1.5 times as long as high. Tarsi I and II each with a single club-like seta in front of lateral disti-dorsal seta. Two claws on all tarsi of known forms.

Type. Isobactrus setosus (Lohmann) 1889 (= *Aletes setosus* Lohmann 1889).

KEY TO NORTH AMERICAN SPECIES (ADULTS)

1a. Claws with a well developed comb which projects medially from shaft of claw. (Note. When the claw is lying on its side, or somewhat obliquely, it may appear to be completely smooth or to have only an accessory tooth.)
setosus (Lohmann) 1889; p. 69.
Connecticut, British Isles, French Atlantic coast, North Sea, Baltic.

1b. Claws completely smooth, lacking even an accessory tooth.

2a. Tarsus with single long seta dorsally near middle of segment. Panelling very pronounced (in Hyrax or glycerine); PD with costae.
hutchinsoni new species; p. 77.
Connecticut.

2b. Tarsus with 2 long setae dorsally near middle of segment. Panelling present, but rather feebly developed; costae absent from PD.
levis (Viets) 1927; p. 74.
Baltic; Connecticut.

Isobactrus setosus (Lohmann) 1889

Figures 54–70

Lohmann 1889a, 326–330, etc.: *Aletes setosus*, new species. Trouessart 1889a, 230: *Rhombognathus setosus* (Lohm.). Lohmann 1893a, 16–18, 20–22, 24, 37, 61, 65, 84: *Rhombognathus setosus.* Trouessart 1901c, 151–152: *Rhombognathus cryptorhynchus*, new species. Viets 1927a, 98, 102–106, 153–156, 158–164, 166–168, 170–171: *Rhombognathus* (s. str.) *setosus.* Viets 1927b, 7, 8–10, 32, 38, 46, 50, 52–55, 65: *Rhombognathus setosus* (Lohm.). André 1939c, 308–310: *Rhombognathus setosus* (Lohm.) 1889 (= *R. cryptorhynchus* Trt.).

Female. Body 294–395μ long, 208–284μ wide, L/W = 1.32–1.49 (av. of 11 specimens, 344 x 242μ, L/W = 1.42). In a female 395μ long (longest measured) the following measurements were obtained: AD 138 x 173μ, OC both 66μ long (true width not discernible because of lateral position), PD 201 x 193μ, AD–PD 95μ, OC–OC 188μ. In a female 294μ long (shortest measured) the following were obtained: AD 108 x 133μ, OC 50 and 46μ long, PD 166 x 166μ, OC–OC 139μ. As the specimen is somewhat distorted, AD–PD can not be measured.

The dorsal plates appear to be somewhat more extensive in the North American form than in the European forms, but they are also quite variable. The general appearance of the mite can be greatly influenced by the amount of compression it undergoes while being mounted, and by the degree of repletion (compare Fig. 54 with 57).

Dorsal plates faintly panelled. PD only rarely showing a faint interruption of the panels in the region occupied by the costae of other species; true costae are never developed. Epimera I and II of opposite sides completely separated by the striated membranous area. Plates I and II on each side are fused along their adjoining surfaces, but I is divided into a broader anterior portion (bearing the first seta) and a narrower posterior portion which is fused with II along its entire posterior margin. Epimeral plates III and IV separated by a narrow band of striate cuticle. Anal plate extremely small, pyriform, subterminal. Setae anterior to first genital sucker apparently internal rather than external. Only 2 pairs of internal suckers are in such a position as to be evident in ventral view, as a rule, since the third pair is usually obscured by the posterior pair of internal spines (but see Figs. 59, 60).

Capitulum completely concealed in dorsal view (Fig. 63). Palpi clearly four-segmented, but all segments very short. Capitulum 64μ long (when seen horizontally) and 70μ wide. Rostrum alone 30μ long and 14μ wide; swollen at middle and bearing 2 pairs of setae. Pharyngeal plate without panels, but with 7 to 9 tendon-like apodemes inserted on each side of mid-line.

Chaetotaxy of legs as follows:

	I				*II*				*III*				*IV*			
	d.	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*
1.	–	–	–	1	–	–	–	1	–	1	–	–	–	–	–	–
2.	1	1	–	–	1	1	–	–	1	1	–	–	1	1	–	–
3.	2	1	1	–	2	1	1	–	2	1	–	–	2	1	–	–
4.	1	1	1	–	1	1	1	–	1	1	1	–	2	1	–	–
5.	1	1	2	1	1	1	2	1	2	1	1	1	2	1	1	1
6.	3	–	–	–	3	–	–	–	3	–	–	–	3	–	–	–

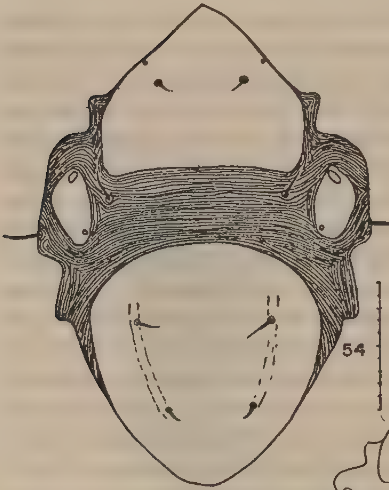
In a female of unknown body length the following measurements were obtained (for I-3, I-5, II-3 and II-5 the height is also given):

	1+2	*3*	*4*	*5*	*6*	*Ambul.*	*Total*
I	41μ	62/50	32	41/41	60	37	273
II	41	62/47	32	43/37	63	38	279
III	49	50	30	41	60	41	271
IV	50	53	30	42	66	38	279

Legs I and II very similar in size and chaetography, but ventral seta of I-2 shorter and more slender than that of II-2 (Figs. 67, 69). I-3 and II-3 only 1.20 and 1.32 times as long as high (swollen). Medial seta of I-5 and II-5 flattened, pectinate. I-6 and II-6 with bacillum and divaricate parambulacral setae, but without prebacillum. Median claw absent from all legs. Lateral claws with comb which projects medially from shaft and which is oriented in the same plane of curvature as outer edge of claw, so that in lateral view the claw may appear to be smooth or to have an accessory tooth but no comb (compare Fig. 58 with 67). III-5 and IV-5 with ventro-medial seta very long, slender, smooth. Parambulacral seta of III-6 reduced to a divaricate seta medially and a pectinate spine-like seta laterally. These are further reduced on IV-6, the medial member being represented by a single rod-shaped seta; outer member heavy and serrate or pectinate as on III-6. Lateral parambulacral seta in some specimens apparently coarsely pectinate, but in others the processes occupy only one side of the seta. In all cases the pectinations or serrations are visible only in favorably oriented tarsi, and in lateral view the appearance is that of a smooth, spine-like seta. All tarsi lack a claw fossa.

Male. Of the more than 50 adults in the author's collection, all are females. These have been collected at different seasons of the year in various localities around New Haven. Many other specimens also have been examined in an unsuccessful search for males, and it is quite possible that males do not exist in this part of the range. Lohmann (1889a: 326–328) made no mention of males, nor did Viets (1927a: 102–106, *etc.*). But André (1939c: 308–310), in a restudy of the type of *Rhombognathus cryptorhynchus* Trouessart 1901, concluded that his single specimen (a male) was simply a specimen of *R. setosus.* At least André showed that claws III and IV had a comb such as that on I and II. The absence of this comb was the character that Trouessart (1901c: 151–152) used to distinguish his "new species" from *setosus.* André's figures show epimeral plates III and IV as contiguous, which is not the case in females of *setosus,* but in other characters André's figures agree quite well with *setosus,* and the present writer can see no reason for rejecting André's conclusion. There are cases known, for example among the Ostracoda, in which certain species reproduce only parthenogenetically in one part of their range but bisexually in other parts. It is not impossible that such is the case in *Isobactrus setosus* also.

Nymphs and larvae. These can be easily distinguished on the basis of the claw characters alone, at least in the northeastern United States.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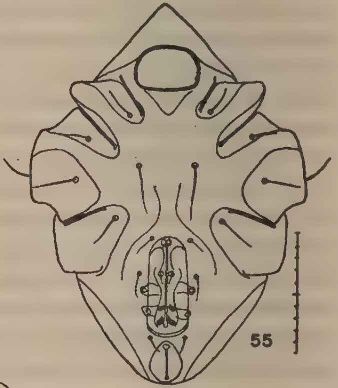
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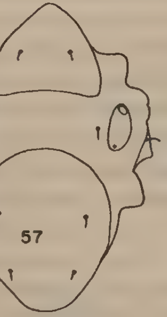
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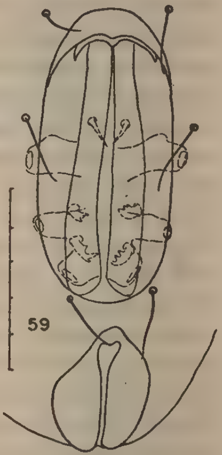
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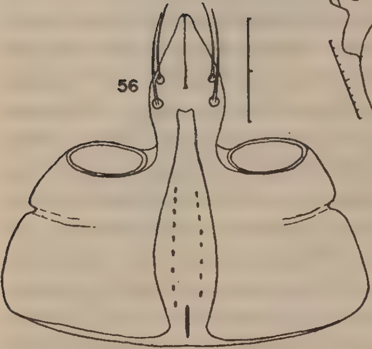
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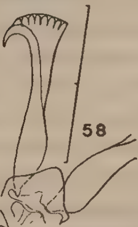
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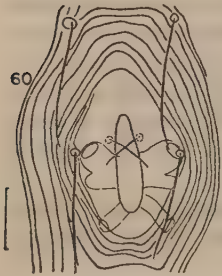
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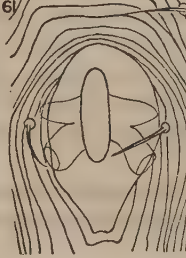
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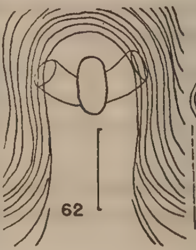
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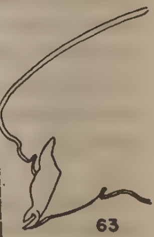
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An unexplained situation is found in the nymphal genital areas. The protonymphs (leg IV with five segments) have a single pair of anteriorly-inclined genital suckers (Fig. 62). Two other types of nymphal genital areas have been found also. In nymphs about 230µ long (leg IV with six segments) there are two pairs of genital suckers (Fig. 61), of which the anterior pair lacks the terminal disc; the posterior pair slopes posteriorly and these have terminal discs. In larger nymphs (ca. 300µ long) there is a third pair of suckers added posteriorly, and the form and position of the four anterior suckers is markedly changed (compare Fig. 60 with 61). This has been verified in several nymphs of each type, and the number, form and orientation of the suckers is constant. In the larger nymphs there is a pair of setae projecting from the genital groove. These can be seen in all specimens. Only one of the smaller nymphs was in a favorable position, and very careful examination showed that there were no setae in the genital groove. No setae could be found here in the poorly oriented specimens either, although they could be seen in the older nymphs almost regardless of orientation. The possibility of a third nymphal stage is suggested but by no means proved by these facts. Although the third pair of internal suckers could be added during the active deutonymphal stage, the addition of a pair of setae appears most improbable.

Remarks. Schulz (1933: 96) expressed doubt that *R. setosus* of Viets 1927 is really that of Lohmann, but he gave no reason for his doubt, and the present writer can see no reason for any. The species is highly variable in the appearance of the dorsal plates (see above), but the ventral armor is very characteristic, and Lohmann's and Viet's descriptions and figures are in close agreement on the details of this.

A peculiar type of carpal structure is found in *I. setosus*, *levis* and *hutchinsoni*, n. sp. Whereas in the other Rhombognathinae the carpite is a distinctly separate sclerite lying between the tip of the tarsus and the middle piece of the claw, the carpite in these three species is fused

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Figures 54–63. ***Isobactrus setosus*** **(Lohmann) 1889.** ***54*** **Female: dorsum.** ***55*** **Female: venter.** ***56*** **Female: capitulum, ventral view (drawn from a slightly compressed specimen in which the capitulum is completely horizontal).** ***57*** **Female: dorsum (rotated).** ***58*** **Female: claw, ventral view.** ***59*** **Female: genito-anal area.** ***60*** **Deutonymph: genito-anal area (drawn from a specimen with a body length of 298µ, leg IV with 6 segments).** ***61*** **Deutonymph: genito-anal area (drawn from a specimen with a body length of 229µ, leg IV with 6 segments).** ***62*** **Protonymph: genital area.** ***63*** **Female: sagittal section (the line is vertical to the horizontal plane of the mite).**

to the end of the tarsus. It is a thin long plate, folded longitudinally down the middle and enlarged distally where it articulates with the middle piece (Figs. 68, 70). The moniliform structure of the basal half would appear to provide greater flexibility of the shaft and to distribute the stress over a greater length of the carpite, insofar as one can judge the value of this arrangement by the examination of mounted specimens. The beads do not represent separate sclerites, but merely local structural differences in a continuous sclerite. This type of carpite probably represents a valid generic character for *Isobactrus*, since it has been found in the three species of *Isobactrus* seen by the writer and is very different from that seen in *Rhombognathides*, *Metarhombognathus*, and also in *Rhombognathus*. The shape of the carpite is approximately the same in the latter as in *Isobactrus*, but the separation from the tarsus is complete. The type of carpite appearing in *Isobactrus* has also been seen by the writer in *Scirus* Hermann 1804, and *Cyta* von Heyden 1826 (Bdellidae). In these genera the moniliform portion of the carpite is longer than in *Isobactrus*. There is, however, no direct relationship between *Isobactrus* and the other two genera.

Distribution. North America: New Haven County, Connecticut (Morris Cove, West River).

French Atlantic, Ireland, North Sea, Baltic.

Isobactrus levis (Viets) 1927

Figures 71–73

Viets 1927a, 98, 103–106, 153–154, 156, 166, 168, 170–171: *Rhombognathus* (s. str.) *levis*, new species. Viets 1927b, 8–9, 46, 53–55: *Rhombognathus levis.*

This species was taken on only one occasion, when four females were obtained. Although very similar to *R. setosus* in general appearance when observed alive and at low magnifications, it attracted attention when first seen because of its movements and the long setae of the tarsi which aided in its recognition under the binoculars. With little material available a full description is not possible but the distinguishing characters of the species will be pointed out. Viets (1927a: 103–106) gave four figures and a detailed comparison with *I. setosus*.

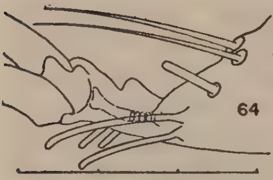
Female. Body 325–353μ long. The specimens were slightly compressed and unusually broad, but the one which appeared most normal was 353 x 229μ (L/W = 1.55) prior to mounting. In this mite the following measurements were obtained: AD 130 x 100μ, OC 48μ long (width not measurable because of lateral position), PD 163 x 149μ. All plates distinctly panelled. Epimeral plates divided as in *I. setosus*, but much more reduced in extent, with all ventral setae lying in the membranous area. Capitulum of same form as in *I. setosus*, completely hidden in dorsal view. In a female with a body 325μ long, the following measurements were obtained: capitulum 53μ long to tip of rostrum and 64μ wide at base; rostrum alone 26μ long and 11μ wide, swollen at middle and bearing 2 pairs of setae just as in *I. setosus*. Palpi 4-segmented.

Chaetotaxy of legs:

	I				*II*				*III*				*IV*			
	d.	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*
1.	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
2.	1	1	–	–	1	1	–	–	–	–	1	–	–	–	–	–
3.	3	–	–	–	3	–	–	–	2	–	–	–	2	–	–	–
4.	1	1	1	–	1	1	1	–	2	–	–	–	2	–	–	–
5.	3	2	–	–	3	2	–	–	1	1	1	–	1	1	1	–
6.	4	–	–	–	4	–	–	–	4	–	–	–	4	–	–	–

Since the legs could be studied only on firmly fixed specimens, it is possible, but not very likely, that some of the setae were overlooked. The complete absence of the dorsal setae on III-2 and IV-2, and the duplication of the long basi-dorsal setae on all tarsi are unusual characters. The latter is especially unusual. These setae appear to be longer than on Viets' specimens, but this is not a significant difference. Medial member of ventral pair of setae on I-5 broad and pectinate, but corresponding seta on II-5 slender and smooth. No setae ventrally on I-6 and II-6. Both I-6 and II-6 with a clavate bacillum, but prebacillum absent from both. Parambulacral setae divaricate and of same form on both I-6 and II-6 (Fig. 71). III-5 and IV-5 without pectinate seta. III-6 and IV-6 with medial parambulacral seta very slender, single; lateral seta also single, but very broad, scale-like and notched. Claw fossa on all tarsi, but best developed on I and II. Lateral membranes absent. Lateral claws scythe-shaped, with neither pecten nor accessory tooth. Median claw absent.

Remarks. This species is distinguishable from *I. setosus* in all stages on the basis of the claw characters alone. It can be distinguished from *I. hutchinsoni*, n. sp., by the less distinct panelling and the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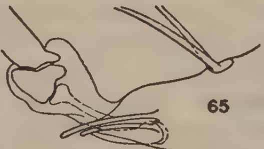
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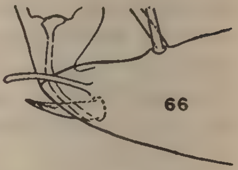
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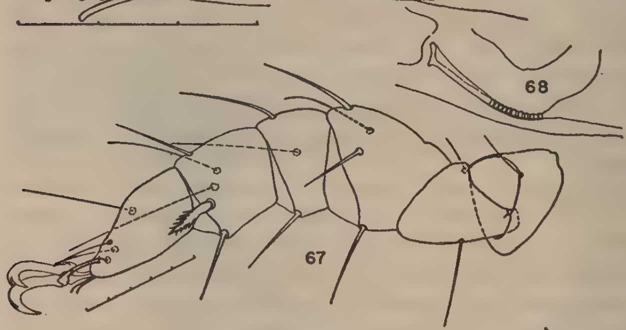
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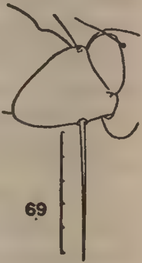
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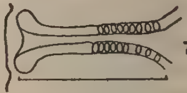
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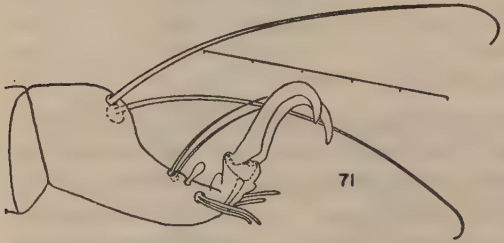
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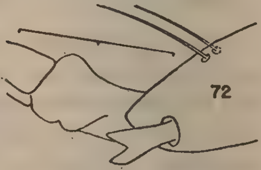
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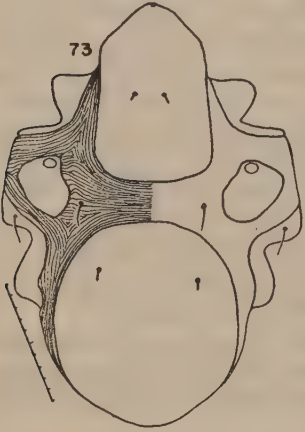
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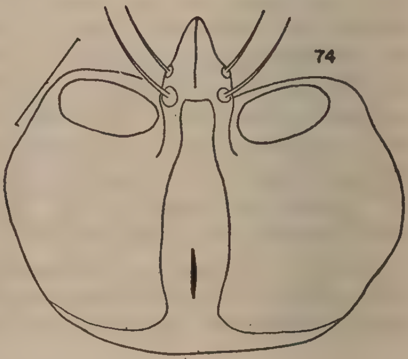
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absence of the costae, which are well developed in *hutchinsoni*. The duplication of the basi-dorsal seta on all tarsi is a unique character. The coxal areas are much less extensive than in *I. hutchinsoni* also, and the setae do not show any marked tendency toward pectination. Other differences will be apparent from the figures and descriptions.

Distribution. North America: New Haven County, Connecticut (Morris Cove).

North Sea.

Isobactrus hutchinsoni, new species

Figures 74–82

Male. Body (7 specimens) 340–375μ long, 215–250μ wide (av. 359 x 237μ); L/W = 1.44–1.58 (av. 1.51).

AD produced over capitulum so that no more than tips of palpi and chelicerae can be seen from above; rounded anteriorly, nearly straight posteriorly. OC somewhat irregular and variable in form, with single round cornea antero-laterally. PD rounded anteriorly, projecting between OC, usually distinctly narrowed behind middle. Setae absent, or so small as to be overlooked easily, even under oil immersion. In a male 353μ long the following measurements were obtained (L/W): AD 126/130; OC 65/61 and 69/58; PD 215/151; AD-PD 23; OC-OC 63μ.

All dorsal plates clearly panelled and finely punctate; numerous pores present (Fig. 78). AD with 7 groups of panels, or only 5 when anterior and lateral groups are coalesced. Panels limited to center of OC and a small area at anterior end. PD with 2 parallel ridges which are finely punctate but not panelled. Membranous areas with parallel striae and very numerous minute hairs (Fig. 82) which can be most easily observed on the margins of the body. The hairs arise from the crests of the striae. A single pair of setae lies in the dorsal membranous area.

Venter as described below for female, except for genital area. A feebly developed genital plate is present on which a small amount of panelling is faintly discernible. In a specimen 370μ long the genital

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Figures 64–70. *Isobactrus setosus* (continued). *64* Female: II-6, lateral view. *65* Female: III-6, median view. *66* Female: IV-6, median view. *67* Female: leg I, median view. *68* Female: carpus of III-6, median view (same scale as *70*). *69* Female: II-2, median view (same scale as *67*). *70* Female: carpite of III-6, ventral view.

Figures 71–73. *Isobactrus levis* (Viets) 1927. *71* Female: II-6. *72* Female: IV-6, lateral view. *73* Female: dorsum.

Figure 74. *Isobactrus hutchinsoni* new species. Capitulum, ventral view.

plate was 93μ long and 70μ wide, with 30 to 32 pairs of setae present (Fig. 76). Anus as in female; not terminal.

Capitulum as described for female. Legs characterized by presence of serrate setae, the long unpaired seta on the tarsi and the slender claws which lack comb and accessory tooth. I-1 with very fine seta medially; I-2 with a dorsal and a ventral smooth seta; I-3 with 4 setae (Fig. 75), all but the dorso-lateral one serrate; I-4 with 3 setae, the lateral one smooth; I-5 with 1 serrate ventral seta, 3 smooth setae and the very conspicuous feather seta. I-6 with a slender, hooked dorsal seta at middle, a pair of serrate setae more distally, a pair of divaricate parambulacral setae and a single minute bacillum at the base of the ambulacrum. Claws smooth as in *I. levis* (Viets) 1927. Leg II identical with I in arrangement of all setae. III-3 and IV-3 with only 3 setae. III-6 and IV-6 with parambulacral setae spiniform, bacillum absent; otherwise III and IV identical with I and II chaetographically. Feather seta on III-5 and IV-5 much longer and more slender than on I and II, but distinctly pectinate. Subterminal dorsal setae on IV-6 often very elaborate. In a male with a body length of 360μ the following measurements were obtained:

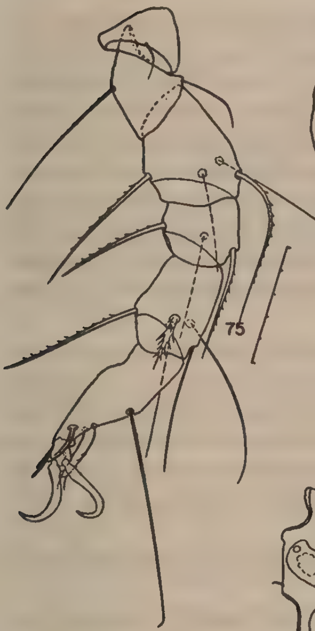
	1+2	*3*	*4*	*5*	*6*	*Ambul.*	*Total*	*T/BL*
I	38μ	53	30	43	55	42	261	.73
II	40	51	30	42	55	43	261	.73
III	50	46	30	42	60	45	273	.76
IV	48	48	30	45	70	45	286	.79

Chaetotaxy of legs:

	I				*II*				*III*				*IV*			
	d.	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*
1.	–	–	–	1	–	–	–	1	–	–	1	–	–	–	–	–
2.	1	1	–	–	1	1	–	–	1	1	–	–	1	–	–	–
3.	3	–	1	–	3	–	1	–	2	1	–	–	2	1	–	–
4.	2	–	1	–	1	1	1	–	1	1	1	–	1	1	1	–
5.	3	1	–	1	3	1	–	1	3	2	–	–	3	2	–	–
6.	3	–	–	–	3	–	–	–	3	–	–	–	3	–	–	–

Female. Body (5 specimens) 346–385μ long; 229–256μ wide (av. 364 x 238μ); L/W 1.50–1.54 (av. 1.53); virtually same size as male. Dorsal and ventral surfaces as in male except for genital area (Fig. 80).

Figures 75–82. *Isobactrus hutchinsoni* (continued). *75* Male: leg I, ventro-medial view. *76* Male: genito-anal area. *77* Male: IV-5 and IV-6, lateral view. *78* Male: dorsum. *79* Deutonymph: dorsum. *80* Female: venter. *81* Deutonymph: genito-anal area. *82* Male: anterior margin of AD at end of costa of right side.



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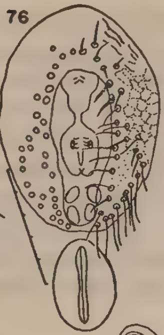

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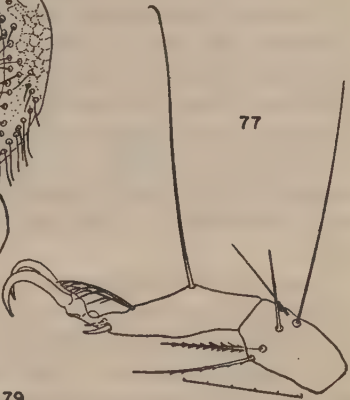

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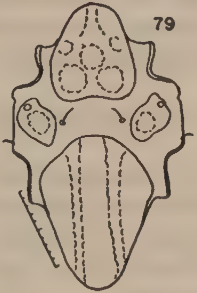

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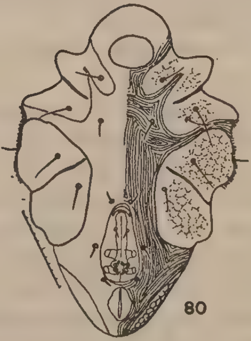

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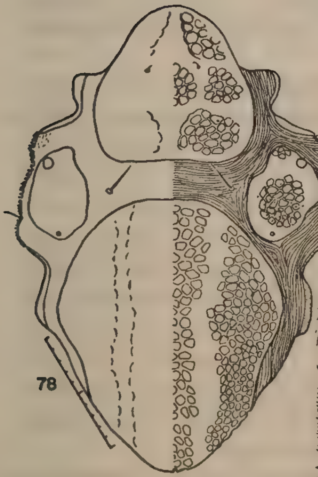

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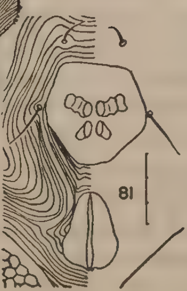

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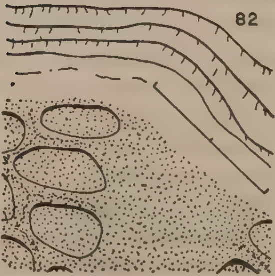

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Venter with epimera I and II of each side fused but completely separated medially from those of opposite side; I not quite divided by the striate membranous area; III and IV also fused completely. Epimera only faintly panelled, the marginal portions of epimera punctate but not panelled and each with a single pair of setae (epimera II in the female drawn showed a duplication of the seta of the left side). Genital area surrounded by 3 pairs of setae. Postero-lateral margins of PD visible ventrally. Anal area separated from genital area by a space only 5–6μ wide. Anus separated from end of body by an interval 0.5 the length of the anal area. Striae well developed, sparsely pilose.

Capitulum 65μ long to tip of rostrum and 75μ at widest part of base; rostrum 26μ long and 14μ wide, bearing 2 pairs of setae. Capitulum very similar to that of *I. setosus*, but base relatively heavier and rostrum relatively shorter. Most of the differences between the figures of the capitula of the two species are more apparent than real, however, and are due in part to the angle from which the structures are drawn. Legs as in male.

Deutonymph. Plates and sculpturing as in adult. Genital area as shown in Fig. 81.

Protonymph. Resembling deutonymph in nearly all respects and easily recognizable by characters of plates and legs. Genital area as in deutonymph but with single pair of suckers. In the one specimen which could be studied there are no setae anterior to the genital area, but the lateral setae are present.

Remarks. This species shows a superficial similarity to *Isobactrus levis* (Viets) 1927, but differs in several important respects. AD is relatively broader and more rounded anteriorly; the panelling on all dorsal plates is much more distinct than in *I. levis.* PD extends anteriorly between OC; the longitudinal ridges are completely devoid of panelling, whereas in *I. levis* the panels cover the entire plate uniformly. In *I. hutchinsoni* the tarsi are apparently more slender, and there is a single long dorsal seta instead of the two setae in *I. levis.* I-3 and II-3 have a large ventral seta which is absent in *I. levis.* The epimera are more extensive than in *I. levis,* I being fused with II, and III with IV; in *I. levis,* I is virtually absent and III and IV are completely separated. The epimeral setae are included in the plates, whereas in *I. levis* they lie in the membranous area.

Distribution. North America: New Haven County, Connecticut (Lighthouse Point, in tidal creek [type locality]).

SUBFAMILY HALACARINAE VIETS 1927

Diagnosis. Middle piece of claw articulating directly with end of tarsus; carpite absent. Palpi 4-segmented, although P-3 and P-4 may be very small or fused, in which case the demarcation between the segments is still visible. Palpi attached to capitulum laterally, so that bases of palpi are separated by an interval considerably greater than width of P-1 and are clearly visible in ventral view. Combined length of P-3 and P-4 greater than ⅓ the length of P-2. Principally marine; rarely fresh water; intertidal to abyssal. Predaceous. Cosmopolitan.

Genus *Halacarus* Gosse 1855

Gosse 1855a, 27, 30: *Halacarus,* new genus. Lohmann 1889a, 270–273, 279, 334–353, etc.: *Halacarus* Gosse. Lohmann 1893a, 67–85, etc.: *Halacarus* Gosse. Lohmann 1901a, 280, 286, 289, 333: *Halacarus* Gosse 1855; "*Ctenopus*—Gruppe." Trouessart 1901a, 253–254: *Halacarus* Gosse 1855. Viets 1927a, 85, 87, 90–91, 115, 116–120, etc.: *Halacarus* Gosse 1855. Oudemans 1939f, 79: *Halacarus* Gosse 1855. Newell 1945a, 58–60: *Halacarus* Gosse 1855.

Diagnosis. Palpi 4-segmented; P-3 with a seta on medial surface which is usually spine-like or rod-like. Palpi rather distinctly geniculate (a line drawn along ventral surface of P-2 in an undistorted palp forms an angle of at least 20°, and usually more than 30°, with a line drawn along ventral side of P-3 and P-4. Sides of rostrum rarely parallel except for a short distance. I-4 and II-4 nearly as long as, or slightly longer than, either segments 3 or 5. Median claw present, carpite absent. Dorsal plates sometimes greatly reduced. Four or 5 pairs of dorsal pores[14] surrounded by a prominent chitinous ring. Typically, one of these is found on AD, one on OC, one between AE and PE near sides of body, and 2 on PD, but when the plates are greatly reduced or absent the pores lie in the membranous area. Cosmopolitan. Marine.

Type. *H. ctenopus* Gosse 1855 (subsequent designation by Viets, 1927a).

[14] Not spiracles, as intimated by Trouessart (1894b: 175).

KEY TO NORTH AMERICAN SPECIES (ADULTS)

1a. Body cylindrical, flexible, the height equal to width. OC and corneae absent; PD divided into a right and a left platelet; AE also divided medially (Fig. 131). Arenicolous............................*anomalus* Trouessart 1894; p. 97.
Connecticut to North Carolina. Also English Channel, North Sea, Baltic.

1b. Body of usual form, broader than high, not flexible. OC present or absent, with corneae present but greatly modified. PD, when present, not divided medially; AE not divided medially (Figs. 83, 84). Not arenicolous.

2a. PD present, bearing the last 2 pairs of dorsal pores. OC well developed, bearing a large pore and with a seta in the indistinct antero-median angle (Fig. 84)....................................*ctenopus* Gosse 1855; p. 82.
Florida. Also Ireland, England (North Sea and English Channel), France, Shetland Islands, Bermudas.

2b. PD absent, pores lying in the membranous area. Cornea present; OC entirely or almost entirely absent, the seta and pore lying in the membranous area.

3a. Anterior pair of dorsal pores at, or slightly behind, middle of AD and posterior to the setae of AD. Genital plate of female with pigmented portion continuous in front of opening, not divided into a right and a left crescentic area. Two pairs of setae at sides of opening and a single pair anterior to GA.....................*actenos* Trouessart 1889; p. 87.
Florida. Also Ireland, English Channel, Bay of Biscay, Cape Verde, Kerguelen.

3b. Anterior pair of dorsal pores very near end of frontal spine and far anterior to the setae of AD. The latter lie outside AD in the adult but in the sides of AD in the larva. Genital plate of female divided into a right and a left crescentic area by a reticulate area which contains 4 or 5 pairs of setae (Fig. 129). Seven to 10 setae lie at sides of genital opening. Below tide zone...............................*frontiporus*, new species; p. 91.
Long Island Sound.

Halacarus (s. str.) *ctenopus* Gosse 1855

Figures 83–93

Gosse 1855a, 28–30, 306: *Halacarus ctenopus*, new species. Lohmann 1893a, 22–23, 81–84: *Halacarus ctenopus*. Viets 1927a, 91, 116, etc.: *Halacarus* (s. str.) *ctenopus*. Viets 1927b, 2, 15–16, 53–55: *Halacarus ctenopus*. Viets 1939c, 550: *Halacarus* (s. str.) *ctenopus*. Newell 1945a, 58–59: *Halacarus ctenopus*.

Male. The two intact specimens in the author's collection measure 471 x 242μ and 450 x 250μ (L/W = 1.80–1.92). In the smaller specimen the following measurements were obtained: AD 158 x 100μ, OC 81 x 42μ and 80 x 37μ, PD 214 x 100μ. Portion of plate anterior to pores only a little more than half as long as the posterior portion; frontal spine not quite reaching to end of I-1 (Fig. 84). Pores situated just behind insertions of leg I on a pair of rather prominent tubercles. Posterior portion of AD faintly panelled, gently rounded, extending to a point just slightly anterior to the large pores on OC. All but central part of plate posterior to pores striate, the striae continuous with those of the membranous area. However, the striae of the plates differ from those of the membranous area in that rows of very minute pores lie in the grooves (Fig. 88). Setae of AD posterior to pores. Ocular plates with single large cornea[15] which is perforated by a minute canal. Cuticle not panelled, but striate like that of AD. A large pore behind middle of plate and a small seta just mediad of cornea. PD reaching to, or nearly to, insertion of leg III; long, ovate in outline, with a pair of large pores and a pair of setae just behind insertions of IV; another pair of pores and setae at end of plate. Central and postero-lateral portions of plate depressed, faintly panelled, most of plate striate like AD. Two pairs of setae in the membranous area between AD and PD. Membranous area faintly striate, the striae very numerous and parallel.

Venter as in female, except for the characters of GA. GA 225μ long and 105μ wide. There appears to be a separation between the genital and anal portions of GA (Fig. 86), but this is probably due to the vertical course of the wall of the plate behind the genital opening. It is doubtful that there is an actual separation. Anterior, lateral and posterior portions of GA striate and porose; remainder of plate (surrounding genital opening) sparsely porose and smooth. Genital opening surrounded by a single row of about 30 small setae (14 to 16 on each side). In addition there is a row of longer setae nearer the margins of the plates. Opening guarded by a pair of slender sclerites.

Capitulum as in female. Palpi (Fig. 89) with P-2 very long and bearing a medial seta at middle of segment in addition to that at the end. P-3 with medial seta rod-shaped and not tapering as shown by

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[15] Viets in his key (1939c: 550) stated: "16 (11) Okularia ± deutlich mit 2 Hornhäuten," which is incorrect, for this would exclude *H. ctenopus*. It should have read "mit 1 oder 2 Hornhäuten."

Lohmann (1893a: pl. 9, fig. 5, male).[16] Although favorably mounted material is not available for study of the legs, the following features were noted. All legs with circularly-arranged striae. Femora I and II with a prominent porose area basi-dorsally. I-3 with a heavy, tapering seta ventrally; I-4 with 2, and I-5 with 4, such setae, all of which are smooth. I-6 identical with that of H. *frontiporus* in that the 2 disti-ventral setae are rod-shaped and rounded terminally. In both species the homologues of these setae on II-6 are tapering. Bacillum and prebacillum both present on I-6, but only the bacillum on II-6. Parambulacral setae on I and II like those of *H. frontiporus*, except that those on II appear to be somewhat shorter than those on I, rather than of approximately equal length. As in *H. frontiporus*, homologues of the heavy ventral setae of I-3, I-4 and I-5 are replaced on II by more slender setae, except for the medial member of the disti-ventral pair on II-5, which is very prominently pectinate. III-2 and IV-2 with a heavy pectinate seta dorsally (Fig. 87, oil immersion).[17] III-6 with 4 setae dorsally, IV-6 with 3. Parambulacral setae in unfavorable position for study, but those on IV-6 of the male definitely pectinate, as in male of *H. frontiporus*. All tarsi with pectinate lateral claws and a median claw. Lateral claws pectinate on legs II, III and IV, but those on I seemingly smooth. However, under oil immersion it can be seen that what is apparently a simple accessory tooth on all the claws is, in reality, the distal end of the comb. Even on I-6, the "accessory tooth" contains from 3 to 5 minute teeth. A similar relationship between comb and accessory tooth is seen in *H. basteri* (q. v.) in which the "accessory tooth" is only the distal portion of the comb, which gives the false impression of being a single large tooth, when seen in side view.

[16] Viets (1939c: 550; 1940g: 1) used the form of this seta in distinguishing between *H. ctenopus*, and *H. oblongus* and *subtilis*.

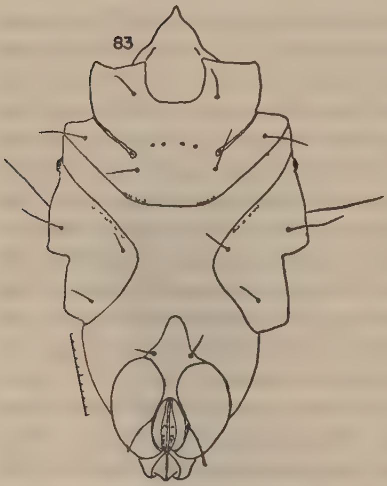
[17] Lohmann (1893a: 83) said of *H. oblongus:* "An beiden Hinterbeinen trägt ferner das 2. Glied am Innenrande einen kräftigen Dorn, der schwach gefiedert ist." There is no seta on the inner surface of III–2 or IV–2 in any halacarid yet studied by the writer (it would be an impediment to the movement of the leg) and there is no doubt that Lohmann meant the dorsal seta (which is never more than slightly dorso-median). Because of Lohmann's statement, Viets (1940g: 6) may have overlooked pectinations on this seta in *H. subtilis*. At any rate, the absence of pectination on this seta in *H. subtilis* and *H. oblongus* must be considered an uncertain key character in distinguishing between *H. subtilis* and *H. oblongus*, for Viets apparently accepted Lohmann's statement without question.

Female. The only female in the author's collection is 547μ long to the tip of the frontal spine and 305μ wide (L/W = 1.79). All dorsal plates approximately same length as those in male, but OC and AD slightly narrower, hence PD relatively (but not actually) shorter. In the male the distance from the anterior end of PD to the fourth pair of dorsal pores (counting the lateral pores) is almost as great (0.94) as the distance from the fourth to the fifth pair of pores. In the female the former distance is only about two-thirds as great (0.63) as the latter. AE undivided, bearing 3 pairs of setae. GA (Fig. 83) containing two roughly crescentic, heavily sclerotized areas at the sides of the genital opening. Anterior portion of plate only faintly demarcated from membranous areas, and bearing a pair of setae. A second pair of setae lies at sides of genital opening.

Capitulum (Fig. 93) 176μ long and 72μ wide; rostrum alone about 100μ long. Base of capitulum only slightly longer than broad. Pharyngeal plate very weakly panelled. Rostrum reaching a little beyond end of P-3, bearing 2 pairs of setae and a pair of minute spines at tips.

Deutonymph. Genital plate completely separated from anal plate, with anterior portion indistinct as in adult. Two pairs of internal suckers, 2 pairs of large setae and a pair of small subgenital setae present (Fig. 92).

Remarks. H. ctenopus, subtilis Viets 1940 and *oblongus* Lohmann 1893 form a group of closely related species within *Halacarus* s. str. The distinctions between these species have not been clearly established owing to errors or to the fact that homologous structures have not received equal attention in the published descriptions of the several species (a very common defect of many descriptions of closely related species). For example, Lohmann's figure of the ventral surface of the female of *H. oblongus* (1893a: pl. 9, fig. 3) shows the homologues of the anterior setae of GA in *H. subtilis* and *H. ctenopus* to lie free in the membranous area, the plate consisting solely of the crescentic areas. But since these three species are so closely related, and since two of the three are known to have a very weakly developed anteromedian portion which includes these setae, the writer hesitates to accept Lohmann's figure as accurate. Similarly, the position of the setae at the anterior end of OC in Lohmann's pl. 9, fig. 1, is questionable. At first glance these setae in *H. ctenopus* appear to lie outside OC, but closer study shows that they lie in the very indistinct anteromedian angle of the plate. Lohmann did not even show these setae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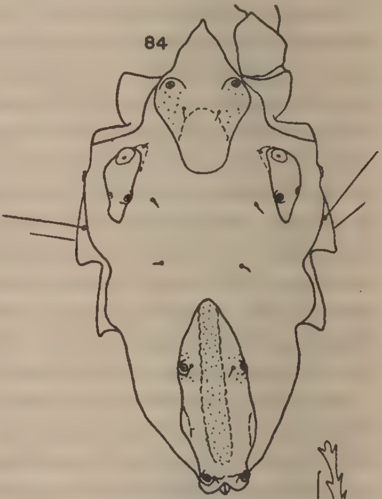
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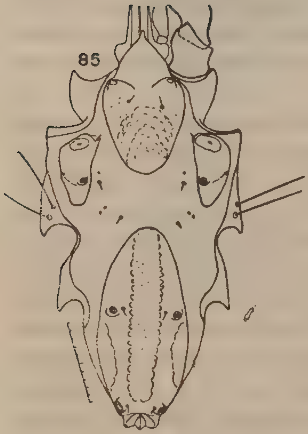
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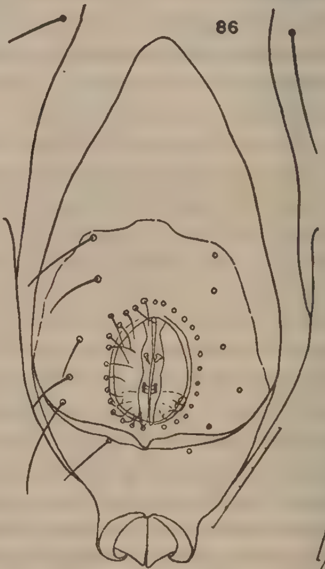
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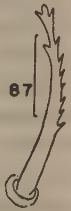
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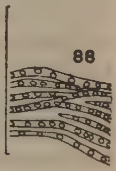
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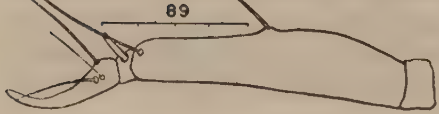
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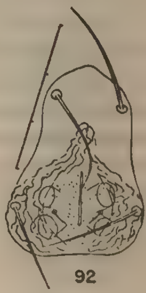
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in his drawing of *H. ctenopus*, so that a comparison is impossible, but in *H. subtilis* they lie in the corner of the plate just as in *H. ctenopus*. These are critical points and are also points in which errors are easily made. It is essential in such cases that homologous structures be compared point for point, at the highest magnifications practicable, and in media of low or high refraction. There is little doubt that these three species differ significantly from each other, but it is equally certain that the differences which are most apparent from the published descriptions and figures cannot be accepted without question. For the present the distinctions can be made principally on the basis of the form of AD and PD of the adult, the published figures of which are probably reliable. Sexual differences must be considered, of course, since they do exist in *H. ctenopus* and *H. subtilis*, and probably in *H. oblongus* (male not yet known).

Distribution. North America: Florida (Biscayne Bay, on Soldier's Key).

North Sea (England), English Channel, Ireland, Bermudas.

Halacarus (s. str.) *actenos actenos* Trouessart 1889

Figures 94–102

Trouessart 1889a, 239–240: *Halacarus actenos*, new species. Lohmann 1893a, 22–23, 66, 83–84: *H. actenos* Trt. Trouessart 1894b, 141, 145–147, 148–151, 156; plate 10: *H. actenos* Trt. Lohmann 1901a, 290, 291: *Halacarus* (*Halacarus*) *actenus* Trouessart 1889. Viets 1939c, 549: *Halacarus* (s. str.) *actenos actenos* Trt. 1889.

This species is also poorly represented in the author's collection, there being only a single male and female and three nymphs. Of these, one of the nymphs has all eight legs, but every one of the legs of the four other mites has been broken off between basifemur and femur, indicating some structural weakness of this joint in this species. These mites were probably dead at the time the material was collected.

Male. The single male is 422μ long to the tip of the frontal spine and 235μ wide (apparently somewhat flattened). AD very indistinct, extending to a point slightly posterior to cornea, bearing a pair of pores and a pair of setae antero-medial to the pores. Portion of AD

Figures 83–92. *Halacarus* (s. str.) *ctenopus* Gosse 1855. *83* Female: venter. *84* Female: dorsum. *85* Male: dorsum. *86* Male: genito-anal plate. *87* Male: dorsal seta of IV-2. *88* Male: anterior portion of GA. *89* Male: left palp, dorsal view. *90* Female: seta of P-3. *91* Male: seta of P-3. *92* Deutonymph: genital plate.

anterior to pores longer than posterior portion, the spine reaching well beyond dorsal seta of I-2. OC greatly reduced, almost invisible even in Hyrax, the corneae very irregular and indistinct. In the male shown in Fig. 97 the plate is simply a small irregular portion of the cuticle which is not striate.[18] There is not even a trace of a postdorsal plate. All dorsal setae and pores behind AD lie in the membranous area, except for dorsal seta of PE.

Ventral surface as in female, except for characters of GA. GA (Fig. 95) pyriform. Genital opening circular, surrounded by 55 or 60 setae (28 + 31 in the specimen drawn) in a single to double row and guarded by a pair of sclerites bearing 5 pairs of setae as shown; 3 pairs of genital suckers present. A pair of setae in the membranous area anterior to plate.

Capitulum (Fig. 94) 134μ long to tip of rostrum and 66μ wide; rostrum alone about 79μ long, extending beyond end of P-2, bearing 2 pairs of setae. Base of capitulum slightly broader than long. Pharyngeal plate not panelled. Palpi typical of the subgenus. Medial seta of P-2 somewhat beyond middle, but variable in position; medial seta of P-3 rod-shaped, blunt distally, less than 10μ long. In the female the latter seta is tapering throughout, pointed at the end and more than 10μ long (compare Fig. 99 with 100). The difference in size probably represents a true sexual difference, but the difference in form is not very clear-cut. Fig. 100 shows that a considerable difference in form of the spine on the two palpi of an individual can

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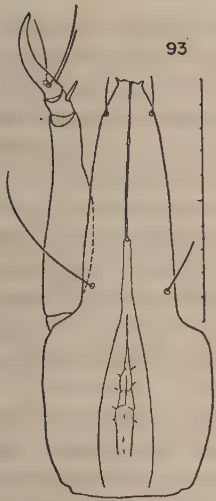
[18] Lohmann (1893: pl. 10, fig. 1) showed only the corneae and stated that the ocular plates were completely absent (as in the female described here by the present writer). Viets (1939c: 549, 550) indicated that Lohmann's figures and statements disagree on the structure of the ocular plate. But an examination of the figures and descriptions of the three species in which Viets claimed this discrepancy to occur shows that there is no discrepancy in Lohmann's statements. Since in all three cases only corneae are present, it is obvious that "Okularplatten" meant, to Lohmann, that part of the plate *outside* the cornea. It is simply a question of terms, and Viets' keys to the species of *Halacarus* s. str. suffer from his failure to make this point clear. Lohmann's description was based on a female, in which there are sunken, rudimentary corneae, but no trace of a plate.

Figure 93. *Halacarus* (s. str.) *ctenopus* (continued). Female: capitulum, ventral view.

Figures 94–102. *Halacarus* (s. str.) *actenos actenos* Trouessart 1889. *94* Male: capitulum, ventral view. *95* Male: genito-anal plate. *96* Deutonymph: genito-anal area. *97* Male: dorsum. *98* Female: genito-anal area. *99* Female: medial seta of P-3. *100* Male: medial seta of P-3 of right and left sides. *101* Deutonymph: cornea of right side. *102* Female: venter.



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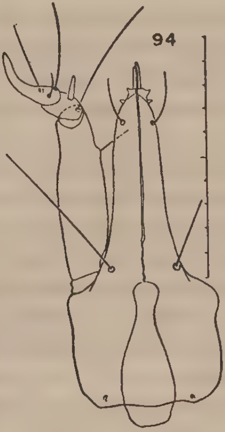

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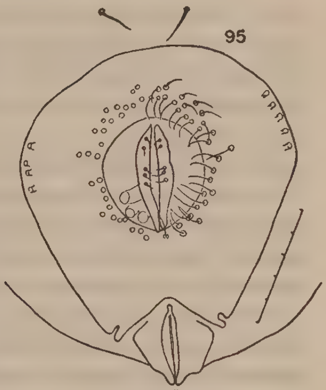

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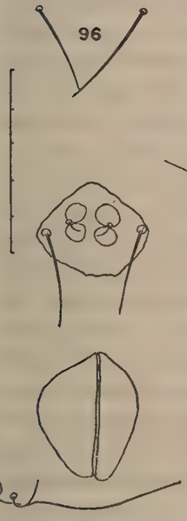

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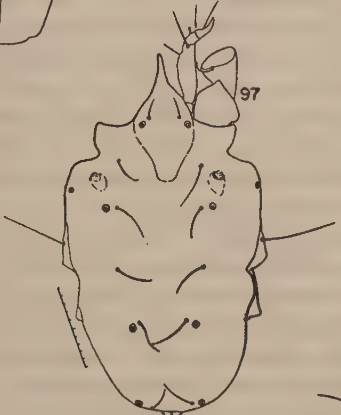

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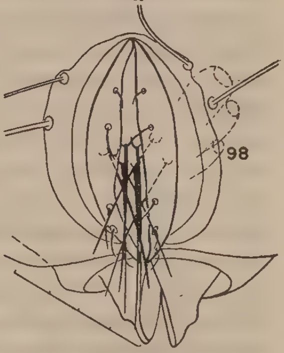

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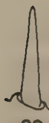

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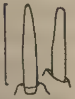

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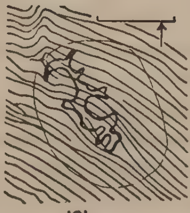

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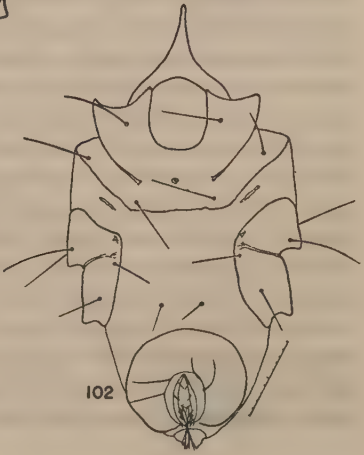

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occur. Slight differences in such characters as this must not be assigned any taxonomic importance, as has been done by some workers, without very close study. Natural variations do occur, and, more important, in the past such structures have been drawn at such low magnifications that an error no greater than the width of a line could cause significant differences in the appearance of the structure.

A recheck on the medial seta of P-3 of *H. ctenopus* and *H. frontiporus* shows that in these species also the seta in the male is appreciably smaller than in the female (Figs. 90, 91, 113, 114), but in all three species P-3 is proportionately smaller in the male than in the female so that there is no special correlation between sex and size of seta, but only the general correlation of body size difference, the male being smaller in these three species.

Female. The single female measured 519μ long to the tip of the frontal spine and 263μ wide (L/W = 1.97). AD as in male, but reaching only to level of anterior margin of corneae. OC completely absent, except for cornea, the latter completely surrounded by striate cuticle. Under oil immersion the cuticle just over the submerged cornea is seen to be reticulate, rather than striate, and the reticulate area is divided by a line which runs diagonally over the cornea. This agrees with Lohmann's description and shows that there is a sexual difference in the degree of development of OC in *H. actenos* just as in *H. ctenopus*. PD completely absent. Setae and pores as in male.

Ventral surface as shown in Figs. 98 and 102. AE undivided. PE with 3 pairs of setae ventrally and 1 pair dorsally. GA without antero-median striate area and with the single pair of setae lying free in the membranous area in front of plate. Heavily sclerotized, pigmented area not divided anteriorly, but continuous. Two pairs of setae at sides of genital opening. Lohmann (1893a: pl. 10, fig. 2) showed one pair here, but since the anterior pair is very slender it may have been overlooked. Trouessart (1894b: pl. 10, fig. 2) showed two pairs. Genital opening guarded by a pair of sclerites bearing 5 pairs of setae. Also, 4 or 5 pairs of long setae (5 according to Trouessart, 1894b) protrude from the opening. Capitulum essentially as in male, q. v. Since the legs were broken off they cannot be described.

Deutonymph. Recognizable by very long, slender frontal spine and complete absence of PD. AD as in adult but slightly smaller. Corneae present, but OC completely absent, the striae passing over deep-lying, atrophied cornea without interruption or change in structure

(Fig. 101). Genital and anal plates completely separate, the genital plate very small; 2 pairs of genital suckers and a pair of minute subgenital setae present (oil immersion). A pair of larger setae lies in the lateral angles of the plate and a second pair lies far anterior to the plate.

The one deutonymph which had not lost its legs was in an unfavorable position for study, but the following features were noted. I-3 and I-4 have a pair of heavy, tapering setae ventrally and I-5 has 2 pairs, all of which are smooth. The medial member of the distal pair of ventral setae of II-5 is pectinate, as in *H. ctenopus.* Dorsal seta of basifemur of all legs smooth. Cuticle of legs not striate, but with a reticular structure similar to, but not so heavily developed as, that on *H. frontiporus.* Median claw extremely small, lateral claws without comb along side of shaft, but under oil immersion it can be seen that the accessory tooth is really not a single tooth but a remnant of the comb containing a few small teeth (as in *H. ctenopus*).

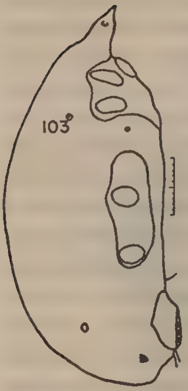
Distribution. North America: Florida (Biscayne Bay, on Soldier's Key).

French Atlantic, English Channel, Cape Verde, Kerguelen.

Halacarus (s. str.) *frontiporus* new species

Figures 103–129

Female. Body 581–665μ long to tip of frontal spine and 346–402μ wide, L/W = 1.68 and 1.65 (2 specimens only). PD and OC absent, except for modified cornea; AD greatly reduced, detectable only by a difference in cuticular markings (Fig. 108). The area enclosed by the dotted lines in Fig. 105 is reticulate and is surrounded by an area about 50μ wide in which the cuticle is irregularly striate. The striae are not of the type usually found in other Halacaridae and they merge almost imperceptibly into the irregular reticulae of the area occupied by AD, and also into the reticulae which cover the rest of the dorsum. Anterior margin drawn out into a sharp frontal spine which projects antero-ventrally (Fig. 103). A pair of anteriorly projecting pores at sides of spine. A single pair of very thick, columellar corneae present (Fig. 125) in dorsal cuticle, but no trace of OC. Three pairs of pores lie posterior to the corneae, the most posterior pair being nearly terminal. Six pairs of very minute setae in membranous area, including that pair which in the larva lies within or at margin of AD.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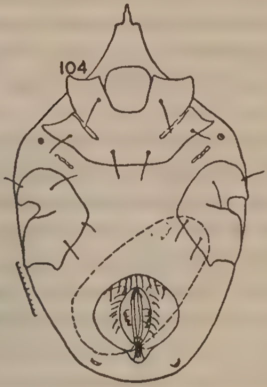
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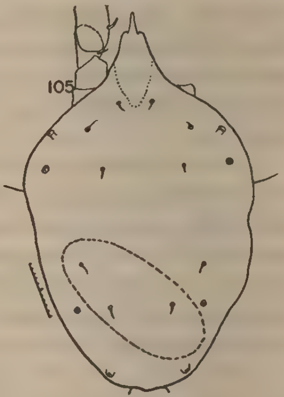
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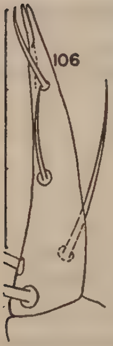
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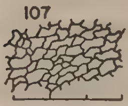
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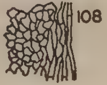
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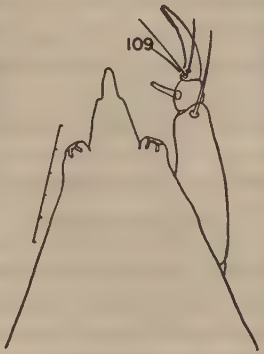
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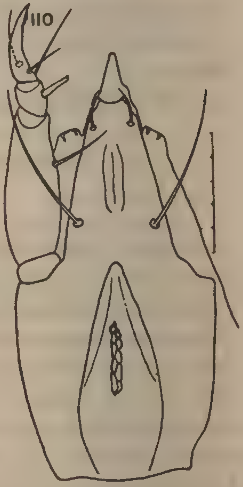
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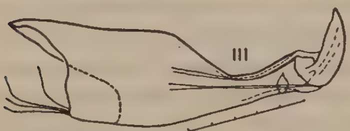
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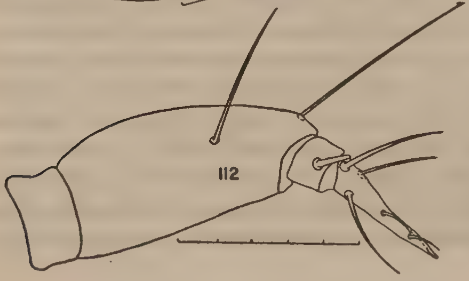
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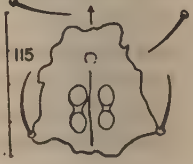
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A large urocyst could be seen inside the body of every specimen examined. In the living mite this is median in position, occupying the excretory duct, but this is usually shifted during preparation of the mite.

AE distinct, undivided medially, with 3 pairs of setae. Epimeral pore absent. PE with 3 ventral setae and 1 lateral seta on each side. AE and PE with very characteristic, irregular panelling (Fig. 123). Membranous area like that of dorsal surface; not with parallel striae. GA (Fig. 129) undivided, broadly pyriform, with the narrower end posteriorly. On each side of genital opening is a large crescentic sclerotized area occupying the greater part of plate. At first glance these sclerotized areas appear to represent the entire genital plate, especially since they are pale brown in color, in sharp contrast with the remainder of GA which is nearly colorless. But closer study shows that the entire pyriform area shown in Fig. 129 is the plate, of which the prominent brown crescentic areas are only a part. Anterior to the opening is a T-shaped reticulate area bearing 8–10 setae; a similar area posteriorly includes the very simple slit-like anus. These two areas are joined by a narrow strip of reticulate cuticle which extends around each side of the genital opening and which bears 7–10 setae on each side. The brown crescentic areas are neither panelled nor porose, but have a characteristic fibrous structure. Remainder of GA reticulate like AD, the membranous area surrounding plate marked in same way as that surrounding AD. A pair of slender, reticulate sclerites guarding opening, each sclerite bearing a seta at each end, with 3 pairs of genital suckers readily visible. Ovipositor with 2 pairs of very long setae which protrude through opening and extend beyond anus.

Capitulum elongate, basal portion rectangular (Fig. 110). In a female with a body length of 658μ the following measurements were obtained: capitulum 157μ long and 81μ wide, the rostrum alone 66μ long and 46μ wide at base. Rostrum very broad at tip, not constricted basally or swollen at middle, extending to or nearly to level of

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Figures 103–115. *Halacarus* (s. str.) *frontiporus* new species. *103* Female: lateral view. *104* Female: venter. *105* Female: dorsum. *106* P-4, medial view. *107* Sculpturing on dorsal surface, near middle of body. *108* Sculpturing on dorsal surface, along right edge of AD. *109* Frontal spine, pores and palp, dorsal view. *110* Female: capitulum and frontal spine, ventral view (capitulum completely horizontal). *111* Female: chelicera. *112* Palp, median view. *113* Female: median seta of P-3. *114* Male: median seta of P-3. *115* Deutonymph: genital area (arrow indicates anterior end).

spine on P-3; 2 pairs of setae as shown in Fig. 110 and a pair of very minute spines at tip. Base of capitulum not swollen, the widest part at base of palpi. Pharyngeal plate with a few degenerate panels. Cuticle sculptured like that on epimera; rostrum smooth. Since the capitulum inclines antero-ventrally it normally appears much shorter than shown in Fig. 110, which is drawn from a female in which the capitulum is horizontal.

Chaetotaxy of legs:

	I				*II*				*III*				*IV*			
	d.	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*
1.	–	–	–	1	–	–	–	1	–	–	1	–	–	1	–	–
2.	1	1	–	–	1	1	1	–	1	1	–	–	1	1	–	–
3.	3	1	1	1	3	1	1	1	2	1	1	–	3	1	–	–
4.	5	1	–	1	3	1	1	1	3	2	1	–	3	2	1	–
5.	6	4	1	1	4	4	2	–	2	4	1	–	2	4	1	–
6.	5	4	–	–	4	4	1	–	3	2	–	–	3	2	–	–

Dorsal seta of I-2 short, spine-like; I-3 with spine-like seta ventromedially and a ventral seta which is thick basally but which tapers quickly to a slender, sharp point. Ventral and medial setae of I-4 and ventral seta of I-5 also tapering rapidly to a sharp point. I-6 with 2 pairs of setae ventrally and 5 setae dorsally, in addition to the parambulacral setae, the bacillum and the prebacillum. Parambulacral setae of usual form; divaricate, rounded terminally. Bacillum and prebacillum *lateral* in position and well formed, except that the latter lacks an alveolus (Fig. 116). Claw fossa absent. Each lateral claw with an accessory tooth and a greatly reduced comb which occupies only the middle third of the inner side of claw and does not reach to the concave margin of the claw. Median claw bidentate, dorsal tooth small. Heavy setae found on I replaced on II by longer, gradually tapering setae, as a rule, with exception of dorsal seta on II-2, which is spine-like. Prebacillum absent, bacillum *medial* in position, parambulacral setae divaricate (Fig. 117). Comb on lateral claws a little longer than on I; teeth of comb much longer and extending beyond concave margin of claw. Setae of III and IV long and slender except for most basal seta of segment 4, which is short and blunt. III-6 and IV-6 without bacillum or prebacillum. III-6 with medial parambulacral seta divaricate; lateral seta single. Ventral member of medial seta sometimes slender and tapering rather than as shown in Fig. 118. In two of the four females examined the ventral member was rod-shaped on both third legs; but in one specimen the same seta was rod-shaped on one leg, tapering on the other, and in the fourth specimen it was tapering on both legs. Claws as on II. IV-6 (Fig. 119) with parambulacral seta reduced to a single tapering seta on each side (compare with male). Lateral claws smooth; dorsal tooth of median claw weakly developed. Claw fossa absent. All legs with epicuticle greatly thickened, reticulate, the reticulations of the same form as those on AD. Femora I and II 1.84 and 1.95 times as long as high (moderately swollen).

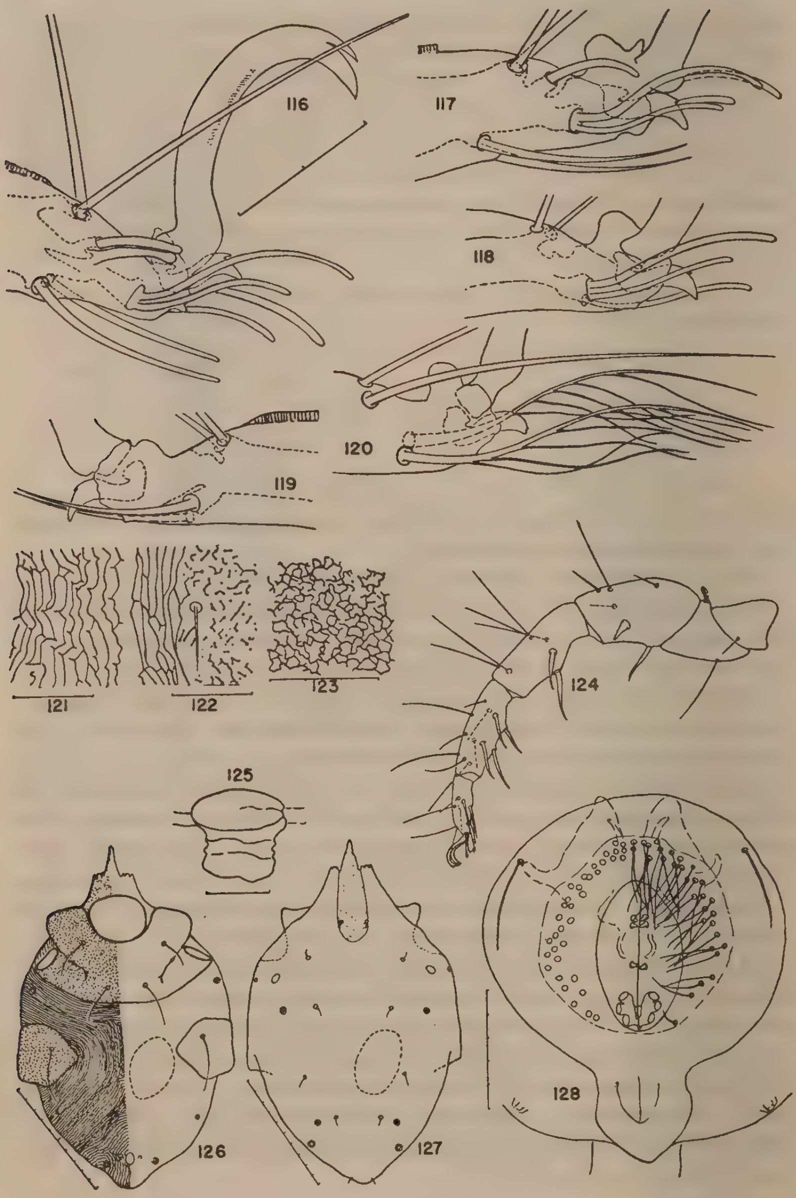
In a female of unknown body length the following measurements were obtained:

	1+2	*3*	*4*	*5*	*6*	*Ambul.*	*Total*
I	88μ	138/75	133	120	71	40	590
II	73	103/53	96	95	75	46	488
III	101	90	95	111	85	55	537
IV	116	110	110	131	95	58	620

Segment 4 of all legs approximately of same length as segments 3 and 5, or only slightly shorter or longer.

Male. Resembling female in most respects except in characters of GA and of tarsus IV. The only male available for measurement is 520μ long and 319μ wide (L/W = 1.63); probably somewhat smaller than female as a rule. Parambulacral seta of IV-6 elaborately pectinate (2 specimens) as shown in Fig. 120, not simple as in female. A similar condition is found in *C. punctatissimus* (Fig. 209). GA (Fig. 128) pyriform as in female, cuticle reticulate, with a single pair of setae within the ring-like reticular area. Inside the latter is another ring-like area bearing from 29 to 35 setae on each side. Cuticle in this part of plate punctate, but not reticulate. Opening guarded by 6 spine-like setae; 3 pairs of internal suckers at posterior end of opening.

Deutonymph. Resembling adult in most respects except in size and genitalia. AD more distinct than in adult and relatively larger, since the setae lie closer to the margins of the plate and are subterminal rather than terminal in position (with reference to the plate). Genital plate (Fig. 115) completely separated from anus by an interval about as long as plate itself (probably varies with age). Outline of genital plate very irregular, cuticle minutely reticulate; a pair of setae at lateral corners of plate (these may be outside the plate) and a second pair in the membranous area antero-laterally from plate. No subgenital setae were found.



Larva. AD long, narrow, distinct, relatively longer than in adult (since it includes the setae which in the adult lie well outside AD). Cuticle with incomplete reticulae represented by minute papillate elevations which are usually joined by narrow ridges to form short chains. Membranous area marked with maze-like striae (Fig. 121); only at the margins of the body do parallel striae appear. Five pairs of setae lie in the membranous area. OC completely absent, except for the highly modified cornea; PD absent. AE not divided medially, with only 2 pairs of setae. PE with a single pair of setae ventrally and no lateral setae. Sculpturing on AE and PE identical with that of AD. As shown in Fig. 126, part of the venter is marked with parallel striae, but the central and posterior portions are marked with maze-like striae such as are found on the dorsum (Fig. 121). Two pairs of pores and a pair of refractile bodies (behind leg III) are present. Legs with 5 segments. Claws II and III with an accessory tooth and a very weak comb (oil immersion); I apparently smooth but not in a good position for study.

Distribution. North America: Rhode Island (three miles north of Block Island, at 34 meters).

Halacarus (s. str.) *anomalus* Trouessart 1894

Figures 130–142

Trouessart 1894b, 141, 143, 156–159: *Halacarus anomalus,* new species. Schulz 1935a, 84–86: *Halacarus anomalus* Trt. 1894. Viets 1939c, 548: *H.* (s. str.) *anomalus* Trt. 1894.

Female. Body 290–353μ long to base of capitulum and 422–465μ long to tip of rostrum. In a female 312μ long the body is 138μ wide (L/W = 2.26). In a female 318μ long the body is 129μ high (L/H = 2.42). Body cylindrical and very flexible. Plates greatly reduced.

AD (Fig. 132) with a pair of minute pores and a pair of setae. PD (Fig. 133) divided into a right and a left half, each platelet bearing a pore at each end and a seta at the posterior end. The panel-like structures seen in the figure are not panels but are areas of muscle insertion.

Figures 116–128. *Halacarus* (s. str.) *frontiporus* (continued). *116* Female: I-6, lateral view. *117* Female: II-6, median view (same scale as *116*). *118* Female: III-6, median view. *119* Female: IV-6, median view. *120* Male: IV-6, median view (same scale as *116*). *121* Larva: sculpturing on dorsal surface, near middle of body. *122* Larva: sculpturing on dorsal surface, along left edge of AD, at level of seta. *123* Female: sculpturing on AE. *124* Female: leg I, median view. *125* Cornea (drawn as a partially sectioned object). *126* Larva: venter. *127* Larva: dorsum. *128* Male: genito-anal plate.

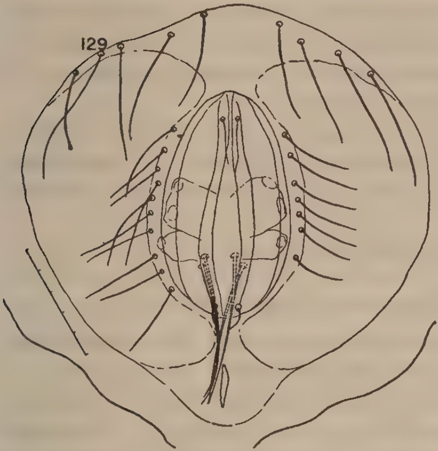
OC and corneae absent. AE (Fig. 131) divided medially, with the usual 3 pairs of setae; epimeral pore large. PE (Fig. 135) with only the 3 ventral setae. Genital plate separate from anal plate, completely divided into right and left halves, each bearing 2 setae on posterior half. A separate sclerite (folded in figure) between genital opening and anal papilla. All plates of body minutely porose.

Capitulum (Fig. 137) 130–140µ long to tip of rostrum. Rostrum alone about 70µ long, not reaching to end of P-2 (*i. e.*, the disti-dorsal end). P-1 to P-4, in a female with a body length of 353µ, as follows (L/H): 13/13, 64/11, 6/7, 24/5µ. P-2 not as high as P-1 and nearly six times as long as high; without setae. (Trouessart [1894b: pl. 10] showed a dorsal seta, but this is probably erroneous. The present writer has examined several specimens closely, and all lacked both the dorsal and the medial seta.) P-3 with a heavy, spine-like seta medially, P-4 with 3 basal setae. Combined length of P-3 and P-4 approximately half that of P-2.

I-1 and II-1 apparently without medial seta. Ventro-medial seta of basal half of I-5 and I-6 spiniform. I-6 (Figs. 140, 141) with bacillum and prebacillum on inner surface of the large lateral membrane of the claw fossa and difficult to distinguish because they are closely applied to each other and to the edge of the membrane. Parambulacral setae double laterally, single medially. Lateral claws with accessory tooth, not pectinate. Median claw unidentate. Leg II without spiniform setae but with a heavy pectinate seta ventro-medially on II-5. Claw fossa very pronounced, the height of the tarsus decreasing sharply beyond the disti-dorsal setae, the membranes only feebly developed. Bacillum lateral, very large, strongly arched and not lying in contact with the membrane; prebacillum absent (Fig. 142). Parambulacral setae single on both sides of tarsus. Lateral claws as on I but considerably longer. III-4 with 1 pectinate seta disti-ventrally; III-5 with a pair of these (Fig. 139). III-6 with claw fossa less pronounced than on II-6; membranes absent. Parambulacral setae single and tapering on each side of tarsus. Pectinate setae and parambulacral setae of IV just as on III.

Figure 129. *Halacarus* (s. str.) *frontiporus* (continued). Female: genito-anal plate.

Figures 130–137. *Halacarus* (s. str.) *anomalus* Trouessart 1894. *130* Female: genito-anal area. *131* Female: ventro-lateral view. *132* Female: antero-dorsal plate. *133* Female: PD of right side. *134* Female: AE of right side, ventral view (same scale as *135*). *135* Female: PE of right side, ventral view. *136* Female: palp, lateral view. *137* Female: capitulum, ventro-lateral view.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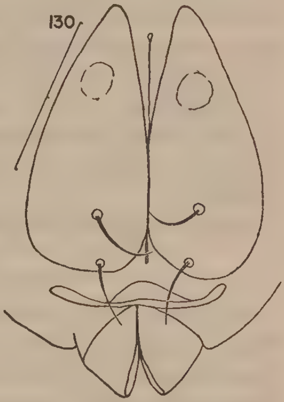
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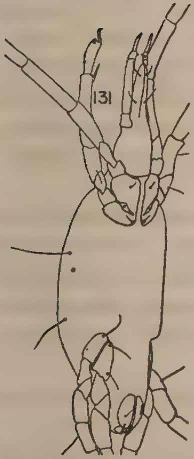
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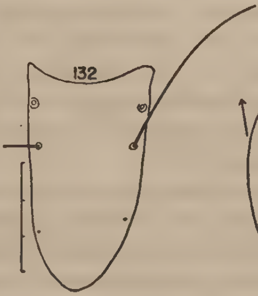
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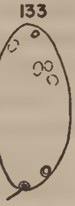
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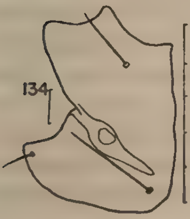
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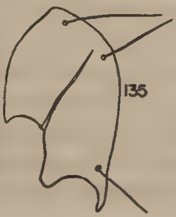
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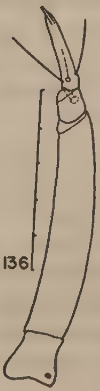
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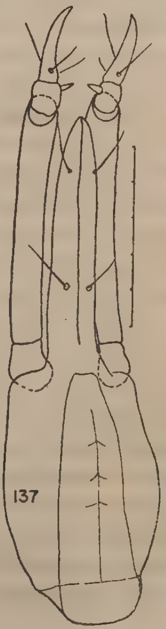
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Male. No males are in the author's collection, although several have been seen. They are distinguishable from the female by the numerous setae around the genital opening. Trouessart (1894b: pl. 7) gave a figure of the genital area of the male.

Distribution. North America: St. Andrews, New Brunswick; New Haven County, Connecticut (Pine Orchard, Morris Cove, South End); Solomon's Island, Maryland; Beaufort, North Carolina (Piver's Island).

France (English Channel), North Sea, Baltic.

Subgenus *Thalassarachna* Packard 1871

Packard 1871a, 108: *Thalassarachna,* new genus. Trouessart 1888a, 755: *Leptopsalis,* new genus. Canestrini 1891a, 708: *Leptosalis* (a *lapsus calami*). Lohmann 1893a, 67–68, 80–84: "*Spinifer*-Gruppe." Trouessart 1893d, 257–259: "Section des Spiniger." Trouessart 1894a, 169: "Groupe '*Spinifer*' de Lohmann (1893)." Trouessart 1894a, 174: *Leptospathis,* new name. Trouessart 1896c, 334: "groupe '*Murrayi*'." Lohmann 1908a, 10: "*Balticus*-Gruppe." Police 1909a, 420: "gruppo *balticus.*" Trouessart 1914a, 8: "Groupe *Balticus* Lohmann." Viets 1927a, 87, 91, 116, 120: *Halacarellus,* new genus. Schulz 1933, 100: "*Halacarus balticus*-Gruppe." Viets 1940g, 62, 75: *Leptopsalis* Trt. 1888; and *Leptospathis* Trt. 1894. Newell 1945a, 58–62: *Thalassarachna* Packard 1871.

Diagnosis. Characters as in *Halacarus* (s. str.) Gosse 1855 with the following exceptions. Medial seta of P-3 spiniform in nearly all species, but may be reduced to a minute hair-like seta. I-4 and II-4 very noticeably shorter than segments 3 and 5. Dorsal plates never as greatly reduced as in *Halacarus* s. str. and dorsal pores not surrounded by prominent chitinous rings.

Type. *Halacarus* (*Thalassarachna*) *basteri* (Johnston) 1836 (= *Acarus basteri* Johnston 1836).

Remarks. All of the "groups," genera and subgenera given in the above list are synonyms of *Thalassarachna* Packard 1871 because the species which are "typical" of them, or their types, are consubgeneric with *Halacarus* (*Thal.*) *basteri basteri,* the type of *Thalassarachna.* The correct status of *Thalassarachna* has been discussed in detail by the present writer (Newell 1945a: 58–62). It was shown that *Thalassarachna verrilli* Packard 1871 is actually *Halacarus basteri* (Johnston) 1836, and since *H. basteri* is consubgeneric with *H. balticus,* which

Viets designated as type of his subgenus *Halacarellus* (1927a: 91), then *Thalassarachna* and *Halacarellus* are identical. The former has priority and must replace the latter.

The position of *Leptopsalis* Trouessart 1888 and *Leptospathis* Trouessart 1894 has been confused ever since 1894. *Leptopsalis* was established for *Leptopsalis longipes*, which is now properly placed in the subgenus *Thalassarachna*. The genus was monotypic at the time of its erection. In 1894 Trouessart proposed the new name *Leptospathis* to replace *Leptopsalis* Trouessart 1888, which was preoccupied by *Leptopsalis* Thorell 1882. Meanwhile *Leptopsalis chevreuxi* Trouessart 1889 (now *Agaue chevreuxi*) had been acquired by the genus *Leptopsalis* Trouessart. In the course of the change to the name *Leptospathis*, as a consequence of several taxonomic errors by Trouessart, *Leptopsalis* "lost" its genotype[19] and was left with only *Leptopsalis chevreuxi*. Trouessart identified his new name *Leptospathis* with Lohmann's "*Chevreuxi*-Gruppe," which must be considered a synonym of *Agaue*, since the "typical" species of the "*Chevreuxi*-Gruppe," *Agaue chevreuxi*, is congeneric with the genotype of *Agaue* (*A. parva*). All subsequent workers appear to have started with this completely erratic procedure of Trouessart's in evaluating the position of *Leptopsalis* Trouessart and *Leptospathis* Trouessart, for all have synonymized these two names with *Agaue* Lohmann.

The situation is simple. *Leptopsalis* Trouessart 1888a is a synonym of *Thalassarachna* Packard, because its type was *L. longipes* which is consubgeneric with the type of *Thalassarachna*. *Leptospathis* Trouessart was only a new name advanced to replace the preoccupied name *Leptopsalis;* hence it must retain the genotype *Leptopsalis* and the two names must therefore receive identical taxonomic treatment.

KEY TO NORTH AMERICAN SPECIES (ADULTS AND NYMPHS)

1a. AD in all instars drawn out into a prominent frontal spine (Fig. 143). Adults with 4 pairs of setae ventrally on I-5, of which the basal 3 pairs are spiniform. Dorsal plates panelled............. *basteri basteri* (Johnston) 1836; p. 102.
Connecticut, Maine, New Brunswick. Also Greenland, Ireland, European Arctic Ocean, North Sea, French Atlantic coast, Baltic, Black Sea.

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[19] Trouessart (1894a: 170) declared *longipes* Trouessart 1888 a synonym of *Halacarus murrayi* Lohmann 1889. This is erroneous, since *longipes* has priority, regardless of its unsatisfactory original description.

1b. AD not drawn out into a prominent frontal spine; with a broad and short triangular projection at most (Figs. 157, 180).

  2a. Adults and nymphs with 3 pairs of small sclerites, each bearing a seta in the membranous area posterior, medial, and anterior to OC (Fig. 180). Arenicolous.................................*capuzinus* Lohmann 1893; p. 118.
Connecticut; New Brunswick.
Also Baltic.

  2b. Without such sclerites, or at most with a single elongate sclerite behind OC; this sclerite does not bear a seta.

    3a. With an elongate sclerite in membranous area behind OC, between levels of legs III and IV (Fig. 169). Cornea absent. I-3 of adult with 3 long, spiniform setae ventrally (deutonymph with 2 and protonymph with 1 here). Arenicolous................*subterraneus* (Schulz) 1933; p. 112.
Connecticut; New Brunswick.
Also Baltic.

    3b. Without such a sclerite behind OC. Corneae present. I-3 of adult without 3 long, spinelike setae ventrally. Not typically arenicolous.

      4a. Anal papilla distinctly forcipate in appearance (Fig. 196). Posterior pair of maxillary setae borne on base of capitulum. Nymphal genital plate completely separated from anus. Typically subtidal.
longipes (Trouessart) 1888; p. 126.
Long Island Sound. Also French Atlantic coast, North Sea, Baltic.

      4b. Anal papilla not forcipate, scarcely projecting beyond end of body (Fig. 158). Both pairs of rostral setae borne on rostrum. Nymphal GA undivided. Typically intertidal.......*balticus* Lohmann 1889; p. 106.
Connecticut; New Brunswick.
Also French Atlantic coast, North Sea, Baltic.

Halacarus (*Thalassarachna*) *basteri basteri* (Johnston) 1836

Figures 143–154

Johnston 1836, 353–355: *Acarus basteri*, n. sp. Packard 1871a, 107–109: *Thalassarachna verrilli*, n. sp. Giard 1888, 512: *Halacarus globosus* Trt. Trouessart 1888a, 754–755: *Halacarus ctenopus* (Gosse). Lohmann 1889a, 271, 343–345, and numerous other pages: *Halacarus spinifer* n. sp. Trouessart 1889a, 244: *Halacarus spiniger*. Trouessart 1889a, 238: *Halacarus ctenopus* (partim) Trt. Trouessart 1894a, 169: *Halacarus globosus* Trt. 1886. Lohmann 1901a, 279, 286, 301: *Halacarus verrilli* (Packard) 1871. Lohmann 1901a, 276–279, 290, 292: *Halacarus* (*Halacarus*) *basteri* (Johnston) 1836. King 1914, 138: *Bdella basteri* Johnston 1847. Viets 1927a, 120, 134, *etc.*: *Halacarellus basteri basteri* (Johnston) 1836. Thor 1931e, 61: *Bdella basteri*.

André 1928c, 2–3: *Halacarus* (*Halacarellus*) *basteri* Johnston. André 1934e, 146: *Bdella Basteri* Johnston 1836. Gimbel 1938, 1–7: *Halacarellus basteri basteri* (Johnston). Viets 1940g, 10: *Halacarellus basteri basteri* (Johnst.) 1836; *Thalassarachna verrillii* Packard 1871. Newell 1945a, 58–62: *Halacarus* (*Thalassarachna*) *basteri* (Johnston) 1836.

Adult. No satisfactory specimens are available for illustrating the entire animal. A good figure of the female was given by André (1927f, after Lohmann 1893a). André also reproduced Johnston's original figures. The appearance of the adult is essentially like that of the deutonymph (Fig. 143).

Palpi (Fig. 145) 4-segmented. P-2 1.54 times as long as P-4. Disti-dorsal seta of P-2 very long, extending well beyond tip of P-3. Spine on P-3 long, thick, more than half as long as P-3.

Chaetotaxy of legs:

	I				*II*				*III*				*IV*			
	d.	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*
1.	–	–	–	1	–	–	–	1	1	1	–	–	–	1	–	–
2.	1	1	–	–	1	1	–	–	2	–	1	–	1	–	–	1
3.	4	2	1	1	4	2	1	1	3	2	1	–	3	2	–	–
4.	4	1	1	1	4	1	1	1	4	1	–	–	4	1	–	–
5.	6	4	3	4	6	4	3	3	6	4	–	–	5	4	–	–
6.	6	8	2	1	6	7	2	–	5	5	–	–	5	5	–	–

I-3 with the ventral setae and the medial seta spine-like. I-4 with the medial seta spine-like as in deutonymph, but with the ventral seta slender and tapering. I-5 with 3 pairs of heavy setae and 1 pair of slender setae ventrally and medially. In the specimen from which Fig. 150 is drawn the distal member of the lateral row (which is usually ventro-lateral in position) had moved ventrally so that it arose very close to the insertion of the distal member of the ventral series. On I-6, in addition to the setae shown in the table, there is a single bacillum just distal to the insertion of the lateral member of the disti-dorsal pair, as in the deutonymph. Parambulacral setae very small, scarcely reaching to end of tarsus. There is probably some variation in the number of setae of the ventral surface, as is the case in the deutonymph. Claws of leg I shorter than those of other tarsi, but with same structure.

The setae of leg II are generally more slender than those of I, although their number and arrangement correspond closely. The principal differences are apparent from the tables and the figures. Bacillum on medial membrane rather than on lateral membrane of claw fossa. Parambulacral setae divaricate. The principal chaetographic feature of III and IV is in the disti-ventral pair of setae of segment 5. The medial member of this pair is heavier and shorter than the inner member of the pair. There is a single parambulacral seta on each side of tarsi III and IV.

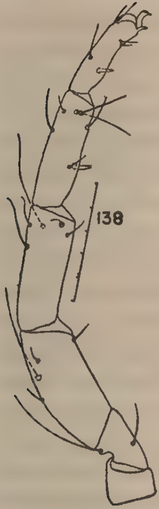
Deutonymph. Dorsum as shown in Fig. 143. AD with prominent frontal process. Genital and anal plates separated by considerable distance (1.5 times length of genital plate in older nymphs). Genital plate wider posteriorly than anteriorly, with 1 seta at each corner and 2 pairs of subgenital setae; 2 pairs of internal suckers present. Palpi and chelicerae as in adult but smaller.

Median and ventral setae on I-3 and I-4 spine-like (Fig. 152), but ventral seta of I-4 more tapering than the others. I-5 with 2 spiniform setae and a long seta ventrally and medially, the medial member of each pair being smaller. Bacillum and parambulacral setae as in adult. Carpus very short, carpite absent. Median claw bidentate. Lateral claws short, heavy, with distinct comb and an *apparent* accessory tooth.[20] Claw fossa well developed; membrane equally well developed on each side of fossa and bearing the disti-dorsal setae of I-6. Bacillum curved ventrad so that it lies close against the lateral membrane of the claw fossa (difficult to find). Chaetography of II nearly

[20] Lohmann (1889a: 344) interpreted the comb as a double comb, which would lead one to believe there was a separate comb on each side of the claw. Actually, there is a single J-shaped comb, the long arm of which extends down that side of the lateral claw which is nearer the median claw, bends smoothly around the end of the claw, and extends up the other side for about one-third the length of the claw. This is shown in Fig. 147, which is an oblique view from below, and Fig. 148, which is a direct ventral view of the claw. From these it is apparent that the accessory tooth in this species is an illusion, it being simply the most distal teeth at the end of the canopy-like comb. In other forms, of course, this is not true, since there is usually a distinct accessory tooth which is developed as the enlarged terminal tooth of the comb, or as an isolated tooth when the comb is absent.

Figures 138–142. *Halacarus* (s. str.) *anomalus* (continued). *138* Female: leg I, lateral view. *139* Female: III-5 and III-6, lateral view. *140* Female: I-6, disti-lateral view. *141* Female: I-6, medial view (bacillum and prebacillum omitted). *142* Female: II-5 and II-6, medial view (bacillum is lateral in position).

Figures 143–149. *Halacarus* (*Thalassarachna*) *basteri basteri* (Johnston) 1836. *143* Deutonymph: dorsum. *144* Deutonymph: ocular plate. *145* Female: palp, median view. *146* Deutonymph: chelicera. *147* Deutonymph: inner lateral claw of leg II, ventro-lateral view. *148* Outer lateral claw, ventral view. *149* Deutonymph: genital plate.



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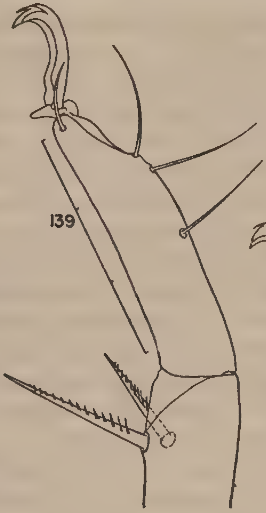

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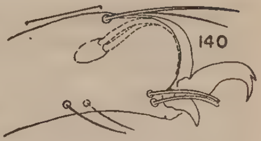

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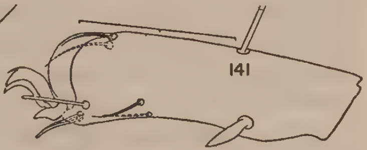

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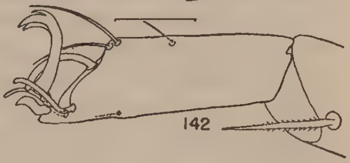

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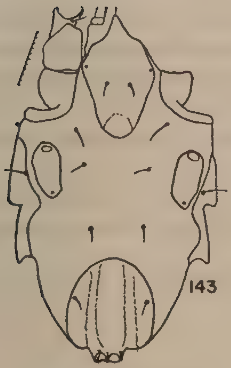

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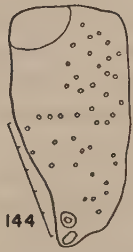

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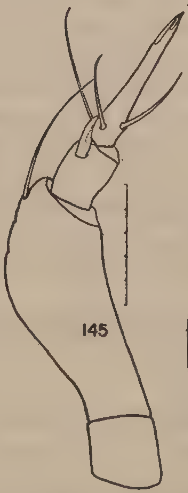

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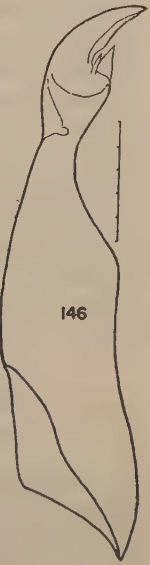

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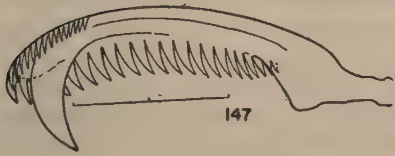

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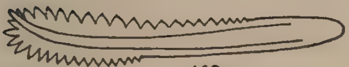

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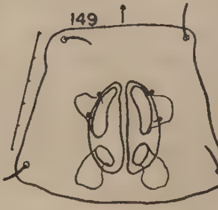

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identical with that of I, but the spiniform setae of I are here reduced to long, stiff, tapering setae (Fig. 153). The proximal ventral seta of II-5 is unpaired and the distal pair of setae is longer and heavier than the proximal, whereas on I-5 the distal pair is the smallest. III-6 with 5 setae dorsally, in addition to the bacillum, which is on the medial membrane of the claw fossa rather than the lateral, and is more erect than that on I-6. The ventral setae show considerable variation, there being from 3 to 5 setae here, judging from the material available (1 unpaired plus 1 paired, 1 unpaired plus 1 paired plus 1 unpaired, or 1 unpaired plus 2 paired, the basal member always being unpaired, with 1, 1½, or 2 pairs of setae distally). In addition there are the divaricate parambulacral setae. There are no special chaetographic features on III and IV. The parambulacral setae are simple, there being a single seta on each side of the tarsus. A prominent claw fossa is found on all tarsi, and membranes are also present.

Remarks. This was the first halacarid to be described from our shores, having been described by Packard in 1871 under the name of *Thalassarachna verrilli.* The present writer has elsewhere (1945a) established the identity of Packard's mite and has discussed the taxonomic significance of its rediscovery. This subspecies can be separated from the other subspecies by means of Viets' key (1940g: 10). Thor (1931e: 61) erroneously listed this species as being synonymous with *Molgus (Molgus) littoralis* (L.) 1745.

Distribution. North America: St. Andrews, New Brunswick; Casco Bay, Maine; New Haven County, Connecticut (Double Beach; South End).

Greenland, French Atlantic, English Channel, British Isles, North Sea, Baltic, Black Sea.

Halacarus (Thalassarachna) balticus Lohmann 1889

Figures 155–167

Lohmann 1889a, 286, 288, 315, 337, 339, 341–343, 345, 359, 368, 384: *Halacarus balticus,* new species. Lohmann 1901a, 291, 293: *Halacarus (Halacarus) balticus* Lohmann 1889. Viets 1927a, 91, 120, 129–131, 153–156, 158, 160–164, 166, 168–171: *Halacarellus balticus* (Lohmann). Viets 1927b, 17–18, 32, 34–35, 45–47, 49–50, 52–55, 65–66: *Halacarellus balticus* (Lohm.). Viets 1940g, 13: *Halacarellus balticus* (Lohm.) 1889.

Female and male of same size, 595–700μ long (av. 665μ) and 380–465μ wide (av. 430μ); body 1.45–1.70 times as long as broad (av. 1.50); based on 8 males and 8 females.

Male. (650μ long.) AD 167μ long and 165μ wide at level of leg I. Anterior margin convex, not produced; lateral margins converging posteriorly, the postero-lateral margin rounded and the posterior margin concave. Conchoidal sculpturing present anteriorly, laterally and posteriorly; remainder of surface only punctate. A single pair of setae near middle of plate.

OC 91 and 100μ long, 75 and 78μ wide; not quite reaching to level of AD anteriorly nor PD posteriorly. Lateral angle a rounded protuberance extending beyond margin of body and visible in ventral view. A pore opens on this protuberance and a second pore is at the posterior end of OC. Single cornea present near anterior margin. Conchoidal sculpturing especially well developed along medial margin but variably developed laterally. PD 346μ long and 256μ wide (1.35 times as long as broad), with a pair of prominent longitudinal ridges. Portions between, and lateral to, ridges depressed and with prominent conchoidal sculpturing. A pair of setae in lateral depressed areas near middle of plate; posterior margin bluntly produced, concealing anal protuberance below. GA and PD completely fused posteriorly, as verified in sectioned material. Dorsal membranous area with 3 pairs of setae. On either side the striations between the two anterior setae and those between the posterior seta and OC are very irregular (even in gravid females). Ocular plates 215μ apart; AD and PD 120μ apart. AE 190μ long, extending to level of seta anterior to III. Cuticle minutely punctate, but neither sculptured nor panelled. Margins of body with slight constriction between AE and PE at level of lateral protuberances of OC.

PE with only 2 pairs of setae ventrally and 1 pair dorsally; panelling present laterally and dorsally, but ventral surface only punctate (as in AE). GA 300μ long and 255μ wide, extending to or slightly beyond level of posterior setae of PE; oval in form. Genital opening 115μ long, surrounded by 125–140 long, slender setae. Genital opening on a raised portion of GA. Most of cuticle punctate, with panelling developed only along lateral margin and posterior to genital area. Opening guarded by 5 pairs of external setae (external position verified in sections). Membranous areas of ventral surface deeply striate except for the spindle-shaped muscle attachment areas between

AE and PE. Striations very irregular near the medial angle of each PE.

Capitulum (Fig. 159) 200μ long and 118μ wide; rostrum 85μ long and 48μ wide at base. (A second male, 680μ long, has a capitulum 218μ long and 125μ wide at the widest part of the base. The rostrum alone was 81μ long and 48μ wide.) Cuticle of base punctate but not panelled. Rostrum smooth, conical, reaching to a point about ⅕ length of P-2 from end of that segment, with a pair of long setae at or slightly beyond level of distal end of P-1, a second pair about ⅕ length of rostrum from end, and a pair of very minute setae at tip. Because of their oblique course, the latter setae appear to be only 3μ long, whereas actually they are 7μ or 8μ long and 1μ thick. Base of rostrum very slightly constricted. Pharyngeal plate bearing 16 to 18 closed cells in an irregular double row which is bordered on each side by a row of 8 to 9 cells which lack distinct outer walls. Chelicerae and palpi as in female.

I-3 with 2 setae ventrally. I-5 with 4 pairs of ventral setae, the basal pair and the outer member of the second pair spine-like.

In one specimen the first three setae on the outer side, as well as the first seta on the inner side, are spine-like. Lohmann (1889: 342) showed considerable variation in these setae. I-6 with an unpaired ventro-median spine. II-5 with 2½ or 3 pairs of setae ventrally. III and IV lacking any special chaetographic features. All tarsi with prominent claw fossa, all claws pectinate and with accessory tooth. A very minute middle claw can be seen on tarsi I and II of some specimens, but this is weakly developed and variable, sometimes being found on only one or two tarsi of an individual. Color in life highly variable, ranging from yellow and orange in young adults and nymphs to brown, gray or nearly black in adults.

Female. Virtually identical with male except in characters of GA. In a female 670μ long, GA measured 263μ long and 263μ wide. Antero-lateral margin at least flattened and usually slightly concave; anterior margin straight or nearly so. Two pairs of setae on genital portion of plate, and a third pair of strongly incurved setae dorsal and

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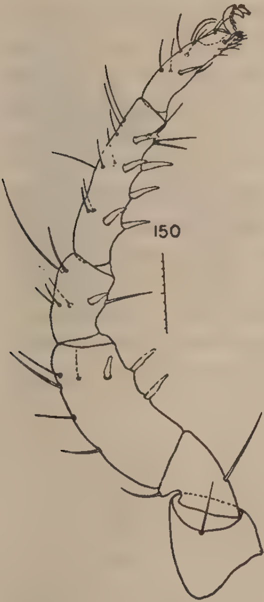
Figures 150–154. *Halacarus* (*Thalassarachna*) *basteri basteri* (continued). *150* Female: leg I, median view. *151* Female: leg II, median view. *152* Deutonymph: leg I, median view (body length 644μ). *153* Deutonymph: leg II, median view (body length 644μ). *154* Deutonymph: ventral membranous area.

Figures 155–156. *Halacarus* (*Thalassarachna*) *balticus* Lohmann 1889. *155* Female: leg I, lateral view. *156* Female: palp, median view.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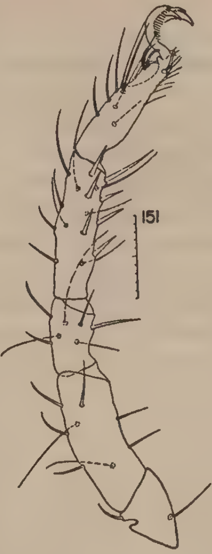
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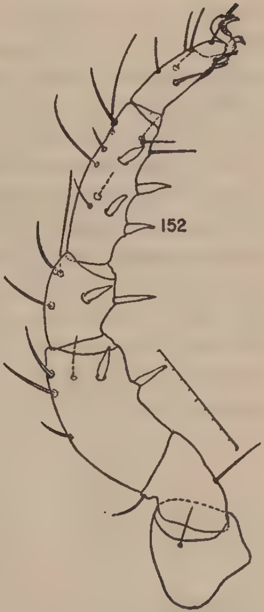
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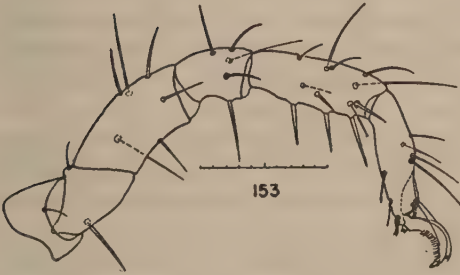
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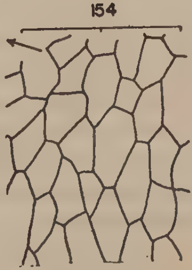
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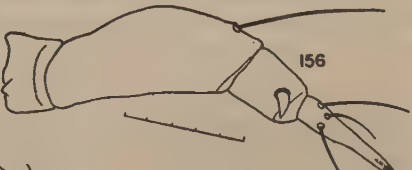
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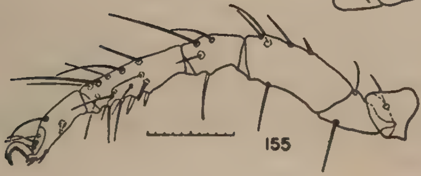
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lateral to anus in region where GA and PD are continuous. Similar setae in male. Oval genital area 141µ long and 106µ wide. GA in younger adult females extending anteriorly beyond IV, but in old gravid females not quite reaching to IV owing to the stretching of the membranous area (cf. Viets 1927a: 122, in which the cephalad extent of GA is used as one diagnostic character).

Palpi, chelicerae and legs as in male. The following measurements and notes are based on a female about 700µ long. Palpi as in most other species of the subgenus. One long seta dorsally on P-2, 3 on basal portion of P-4, and an extremely small seta near tip of P-4. P-4 with 2 small setae closely appressed to sides of tip of segment. P-3 with heavy spine. L/H of P-1 to P-4: 25/31, 83/36, 27/22, 51/10µ. Chelicera 4.9 times as long as high. Leg I with L/H of principal segments as follows:

	3	*4*	*5*	*6*	*Claw*
I	135/55	73/45	131/47	55/28	37/15
II	120/50	63/42	118/38	108/17	48/32
III	116/41	75/37	125/33	128/27	42/32
IV	131/48	75/40	131/35	131/27	43/30

Deutonymph. 425–570µ long. The drawings are made from a specimen 465 x 300µ. Dorsal plates very similar to those of adults. OC projecting beyond lateral margins as in adult; cornea present. GA undivided; 2 pairs of genital suckers present, 2 pairs of setae ventral to anterior suckers.

Protonymph. 310–430µ long. Dorsal plates very similar to those of deutonymph and adult except in size. OC projecting beyond lateral margin, cornea present. GA undivided; a single pair of genital suckers present.

I-3 with only the triangle setae. I-5 ventrally with 2 pairs of setae of which the basal pair is spine-like. Tarsi and claws as in adult. In Figs. 163 and 164, two protonymphs are drawn to the same scale, and from these drawings it is clear that nymphal growth within any

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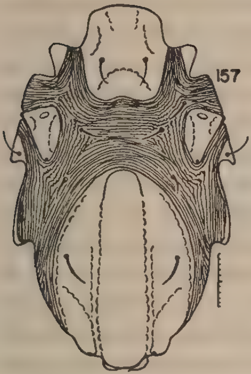
Figures 157–167. *Halacarus* (*Thalassarachna*) *balticus* (continued). *157* Male: dorsum. *158* Female: venter (same scale as *157*). *159* Female: capitulum, ventral view. *160* Female: chelicera. *161* Replete larva: dorsum (body 312µ long, same scale as *162*). *162* Deutonymph: dorsum (same scale as *157*). *163* Replete protonymph: dorsum (body 435µ long, same scale as *162*). *164* Young protonymph: dorsum (320µ long, same scale as *162*). *165* Deutonymph: genito-anal plate. *166* Male: genito-anal plate. *167* Male: I-5 of right side.

Figure 168. *Halacarus* (*Thalassarachna*) *subterraneus* (Schulz) 1933. Deutonymph: genito-anal plate.



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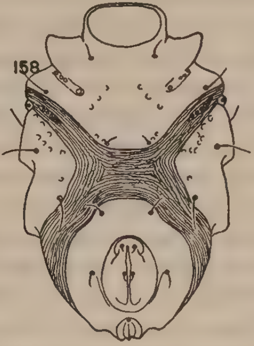

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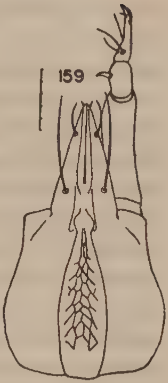

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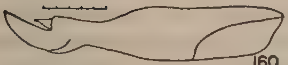

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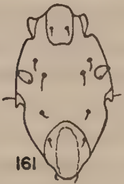

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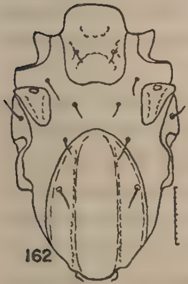

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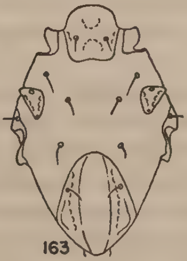

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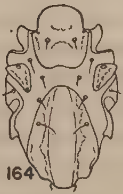

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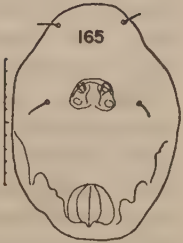

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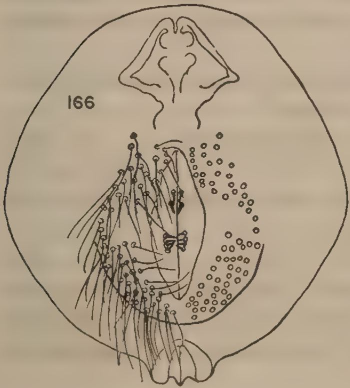

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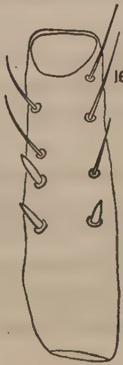

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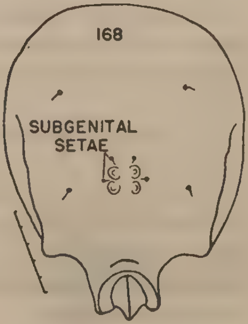

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SUBGENITAL
SETAE

instar in this species occurs only by an increase in size of the membranous areas, the plates remaining the same size throughout the protonymphal stage. The striations in the membranous areas become further separated during growth. Thus in the larger specimen, from which Fig. 163 is drawn, eight striae crossed the dorsal midline in a distance of 30µ, whereas eight striae were found to occupy only 7.5µ in the corresponding position in the smaller mite. Comparing the length of the membranous area between AD and PD in the two mites (ca. 5:1) it is evident that the number of striae remains the same throughout any one nymphal stage, and any increase in numbers of striae occurs only from one instar to the next. The increase in the number of striae from protonymph to adult is appreciable, for in the protonymph the area between OC and II is crossed by about 20 striae, whereas in the adult approximately 30 are found here.

Larva. 180–315µ long. Dorsal plates similar to those of later instars except in size. OC oriented somewhat more transversely than in nymphs, with a pore at each end, but cornea absent. Genital area absent. PE with only the ventral seta. I-3 with only the triangle setae. I-5 ventrally with single pair of filiform setae. Tarsi and claws as in adult.

Remarks. The North American forms key out easily in Viets' key (1940g: 10–15). Several figures are given by Viets (1927b: 21, 22, 32, 34, 35, 45, 65). His fig. 81 does not appear typical, especially in regard to the ocular plates. Also, there are considerably more setae on GA of the male drawn in Fig. 166 than on that drawn by Viets (1927b: fig. 52), but elsewhere Viets (1927a: fig. 68) presented another figure which showed even fewer setae here. It would appear, therefore, that considerable variation in the number of setae on GA occurs in this species.

Distribution. North America: St. Andrews, New Brunswick; New Haven County, Connecticut (Morris Cove).

French Atlantic, English Channel, North Sea, Baltic.

Halacarus (*Thalassarachna*) *subterraneus* (Schulz) 1933

Figures 168–178

Schulz 1933, 100–102, 105: *Halacarellus subterraneus*, new species. Schulz 1935a, 86–87: *Halacarellus subterraneus.* Viets 1936f, 548: *Halacarellus subterraneus* Schulz 1933. Viets 1940g, 13: *Halacarellus subterraneus* Schulz.

Female. Body 450–568μ long, 256–332μ wide, L/W = 1.60–1.84 (average of 10 specimens 490 x 286μ. L/W = 1.71).

Anterior and posterior margins of AD nearly straight as a rule, but posterior margin occasionally distinctly convex, or there may be short postero-lateral margins forming a six-sided plate; lateral margins converging only slightly (Fig. 169); a single pair of setae anterior to the middle of AD. Widest portion of OC about ⅓ length of OC from its anterior end; plates tapering to a rounded point posteriorly; corneae absent, but 2 pairs of pores lie along sides of plates. PD straight anteriorly, with sides converging only slightly and with 3 pairs of setae present. Anus projecting beyond end of plate. Dorsal plates finely punctate; delicate panelling covering most of surface. Membranous areas greatly restricted, with very delicate parallel striae, with a pair of setae anterior to OC, and with a second pair near the antero-lateral angles of PD. A pair of slender platelets between PD and PE which are punctate and occasionally have a few small panels but which bear neither setae nor pores.

AE with right and left halves fused; posterior margin straight; 3 pairs of setae present. PE with 3 pairs of setae ventrally and 1 pair dorsally. GA undivided; 2 pairs of setae outside the oval area. Genital opening about ⅓ length of GA, guarded by a pair of strap-like sclerites extending longitudinally, each bearing 2 minute setae (or 1 seta) at anterior end and a heavier seta behind middle of sclerite. Three pairs of suckers internally, 2 pairs at middle of opening and 1 pair near posterior end; 2 pairs of heavy internal setae between posterior suckers (Fig. 173). These latter setae are on the ovipositor itself and are certainly the posterior 2 pairs of setae which Schulz (1933: 101) associated with the pair near the middle of the band. However, the former are external whereas the latter are internal. Membranous areas restricted and containing 2 (or 3) pairs of sclerites. The largest pairs (the "längliche lichtbrechende Flecken" of Schulz, 1933: 101) are always present and lie between AE and PE and between PE and GA. In addition, there is usually a pair of very minute sclerites at the inner angles of PE. The 2 large pairs serve as muscle attachments. In a female with a body length of 488μ and a width of 291μ, the following measurements were obtained: AD 138μ long, 164μ wide; OC 125 x 58μ, and 126 x 65μ; PD 332 x 201μ; AE 166μ long; GA 256 x 194μ; genital area 97 x 76μ.

Capitulum as in male and palpi of usual form. In one female

(AE 126μ long and 141μ wide) these measurements of P-1 to P-4 were obtained (dorsal L/H): 15/23, 56/37, 22/15, 29/7.5μ (ratios of L/H = 0.65, 1.51, 1.47, 3.87). Chelicerae 153μ long and 40μ high. Base of chelicera relatively short and quite uniformly thick.

Legs very characteristic; chaetotaxy as follows:

	I				*II*				*III*				*IV*			
	d.	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*
1.	–	–	–	1	–	–	–	1	1	–	1	–	1	–	1	–
2.	1	1	–	–	1	1	–	–	1	1	–	–	1	1	–	–
3.	5	3	–	–	5	1	–	–	3	1	–	–	3	1	–	–
4.	3	1	–	1	3	1	–	1	1	1	1	–	2	1	–	–
5.	6	4	–	4	6	3	–	3	3	4	–	–	3	4	–	–
6.	3	2	–	1	3	1	–	–	3	2	–	–	3	2	–	–

I-3 with 2 stiff, blunt setae dorsally and 3 very long, heavy spine-like setae ventrally. Medial seta of I-4 flattened, pectinate. I-5 with a row of 4 setae ventrally, the basal 3 spine-like, the fourth slender and tapering; a similar row of setae found medially. Three of 20 specimens have only 2½ pairs of spine-like setae on one leg (1½ pairs of slender setae), but the other leg has the normal three pairs. It must be expected, therefore, that an occasional individual will be found which has 2½ pairs of spines on each side, but this would have no taxonomic significance whatever if it were found only in isolated instances. The six "dorsal" setae in the above table are not strictly dorsal, but are so designated to avoid confusion with the others. Chaetography of I-6 virtually identical with that of H. *capuzinus*, differing only in relative sizes of the various setae (compare Fig. 171 with 187). Prebacillum not so perfectly formed and appearing to be a flattened expansion of the membrane rather than a distinct seta; although partly hollow, it does not appear to have an external opening. Median claw bidentate, lateral claws completely smooth.

II-3 with only 1 slender seta ventrally. Medial seta of I-4 often faintly pectinate, but not always so. II-5 has only 3 pairs of heavy setae, none of which are as heavy as those on I-5; the medial 3 are pectinate. II-6 with the bacillum but without prebacillum; parambulacral setae well formed. The bacillum is on the medial claw

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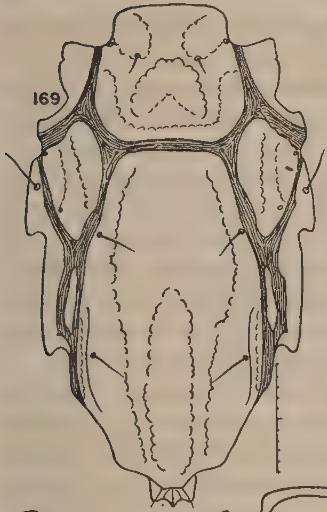
Figures 169–175. *Halacarus* (*Thalassarachna*) *subterraneus* (continued). *169* Male: dorsum. *170* Female: palp, median view. *171* Female: leg I, median view. *172* Female: leg II, ventro-median view (same scale as *171*). *173* Female: venter. *174* Protonymph: leg I (same scale as *171*). *175* Female: leg I, median view.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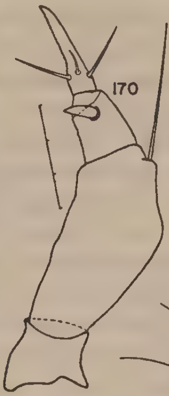
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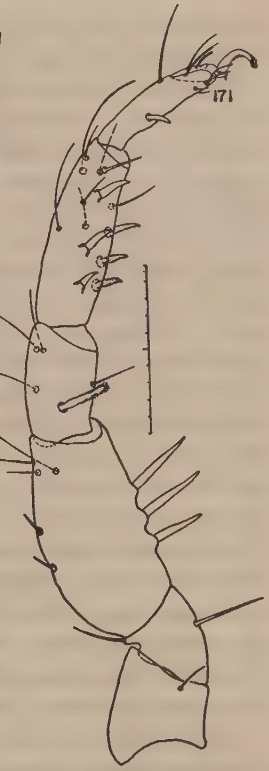
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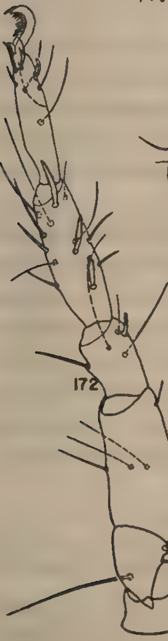
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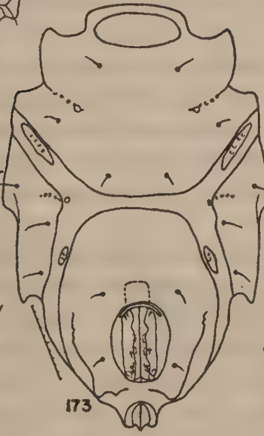
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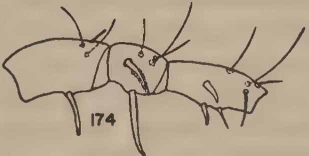
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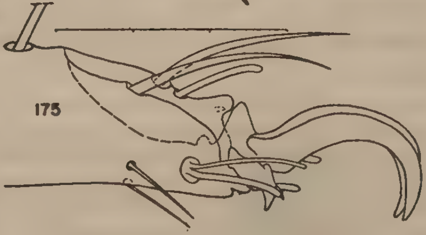
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membrane rather than on the lateral membrane. Median claw not bidentate; lateral claws with comb and a fine accessory tooth.

III-3 and IV-3 with 2 stiff, usually blunt setae dorsally; III-5 and IV-5 with the 3 ventro-medial setae heavy, pectinate, the ventrolateral seta slender, smooth. III-6 and IV-6 without bacillum.

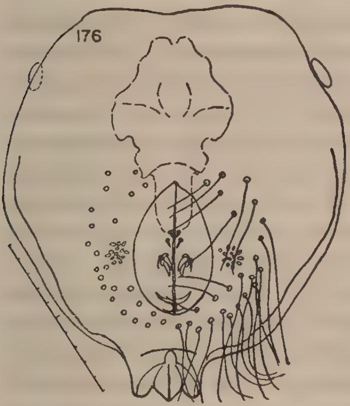
Male. Somewhat smaller than female. Body 422–506μ long, 242–298μ wide, L/W = 1.65–1.74 (average of 10 specimens: 469 x 276μ, L/W = 1.70). Dorsum and venter as in female, except for GA. Schulz (1933: 101) indicated that the posterior platelets between GA and PE are absent in the male, but this was probably due to an oversight. Occasionally in prepared specimens they are turned on edge or pushed under the edge of GA so that they are difficult to see.

GA with 22 to 26 slender setae on each side of the plate. There is also a group of 12 to 15 small refractile spots on each side of the opening which are either pores or large puncta; they are quite irregular in shape and size and usually are disposed in a somewhat radial manner. Genital opening guarded by 5 pairs of heavy setae (Fig. 176). Fig. 178, at a much higher magnification, shows the form and arrangement of the setae more accurately, and shows also the three genital suckers of the right side. Since these face the mid-line they appear as block-like structures rather than circles (compare with *H. capuzinus*). It is difficult to determine whether the setae are external, but they most likely are (see *H. balticus*).

Capitulum (in a male with a body length of 464μ) 139μ long and 95μ wide; rostrum alone 61μ long and 38μ wide just distal to the slightly constricted base (Fig. 177). Tip of rostrum sharp, reaching to, or nearly to, end of P-2. Sides of rostrum converging uniformly toward tip; 2 pairs of setae present and a pair of short, heavy spines at end of rostrum. Pharyngeal plate with about 15 closed cells and 6 to 8 open cells. Palpi as in female. Legs also as in female but with a tendency toward slightly heavier spines and more distinct pectinations.

Figures 176–178. *Halacarus* (*Thalassarachna*) *subterraneus* (continued). *176* Male: genito-anal plate. *177* Male: capitulum, ventral view. *178* Male: genital opening (internal suckers on one side, setae on other).

Figures 179–184. *Halacarus* (*Thalassarachna*) *capuzinus* Lohmann 1893. *179* Female: chelicera. *180* Female: dorsum. *181* Female: venter. *182* Deutonymph: genito-anal plate. *183* Female: leg IV, ventro-medial view. *184* Male: genito-anal plate (same scale as *182*).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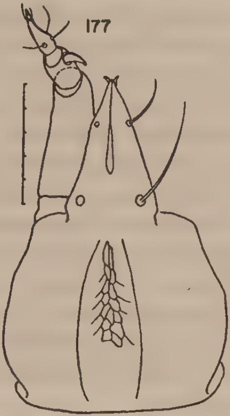
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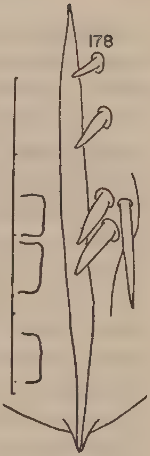
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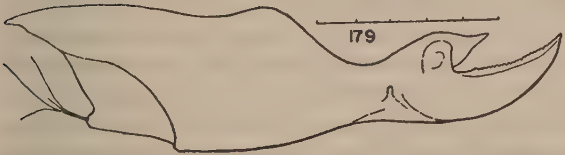
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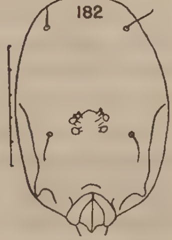
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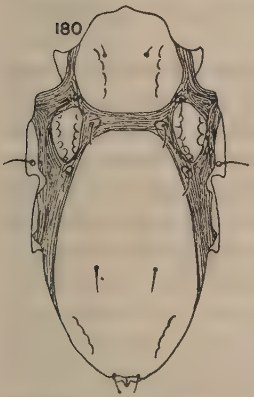
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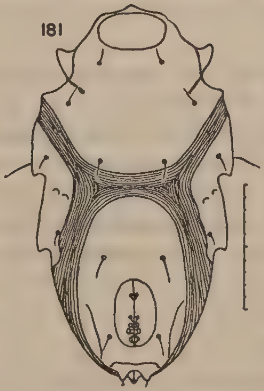
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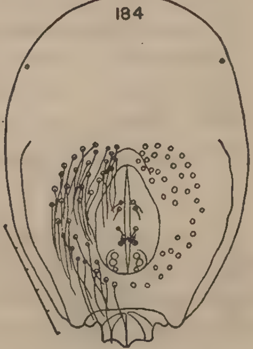
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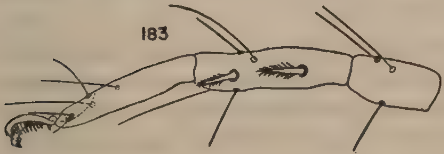
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Deutonymph. Body 360 x 200µ (varying, of course, with age of nymph), closely resembling adult in general appearance. PD rather sharply rounded anteriorly but not truncate as in adult; a pair of platelets between PD and PE as in adult. I-3 with only 2 spines ventrally and with only a single seta dorsally behind the triangle setae. I-4 with single pair of spines ventrally and the triangle setae dorsally. I-5 usually with 3 pairs of setae ventrally and medially, only 2 pairs of which are spine-like. This segment is variable as in the adult. III-5 and IV-5 with 2 small pectinate setae ventro-medially. In one individual a single one is present on III-5 of one side, and 2 on the opposite leg. Platelets between AE and PE and between PE and GA present as in adult. GA undivided; 2 pairs of setae away from genital area and 2 pairs of smaller subgenital setae near the suckers, arranged as shown in Fig. 168.

Protonymph. Easily recognized on plate characters. I-3 with a single ventral spine; I-4 with a very heavy spine-like seta ventrally, which is not only relatively, but actually, longer than in deutonymph or adult (Fig. 174). GA as in deutonymph but with only 2 suckers.

Larva. Most easily recognized by heavy ventral seta on I-4 and the ventral platelets between AE and PE. The dorsal platelets and the ventral platelet between GA and PE are lacking. Legs 5 segmented, segments 2 and 3 fused.

Remarks. There can be little question that this is identical in all significant respects with the European form, although this is not apparent when the present description is compared with the original one of Schulz. The fact that Schulz completely overlooked the very striking platelets behind OC indicates that any discrepancies in the two descriptions probably do not represent real differences. Viets (1936f: 548) showed these platelets to be present in the European form.

Distribution. North America: New Haven County, Connecticut (Morris Cove).

Baltic Sea.

Halacarus (*Thalassarachna*) *capuzinus* Lohmann 1893

Figures 179–191

Lohmann 1893b, 199: *Halacarus capuzinus*, new species. Lohmann 1893a, 16, 21–22, 38, 42–43, 61–65, 82: *Halacarus capuzinus* Lohm. Lohmann 1901a, 290, 292: *Halacarus* (*Halacarus*) *capuzinus* Lohmann 1893. Viets 1927a, 120, 127, 129, 170: *Halacarellus capuzinus* (Lohmann) 1893. Schulz 1933, 98–102, 104: *Halacarellus capuzinus* (Lohmann); *H. capucinus.* Schulz 1935a, 87–88: *Halacarellus capucinus.* Viets 1940g, 13: *Halacarellus capuzinus* (Lohm.) 1893.

Female. Body 290–367μ long, 145–196μ wide; 1.8 to 2.0 times as long as broad. AD 75–80μ long, 80–85μ wide; usually with short, broad antero-median projection. Panelling weakly developed except at margins. Posterior margin nearly straight, the postero-lateral angles rounded. A single pair of setae at about middle of plate. OC 40–50μ long, 25–30μ wide; rather variable in proportions. Anterior margins sloping outward, the sides parallel for a considerable distance or converging posteriorly throughout. Cuticle usually with several conchoidal panels. Anterior end of plates anterior to hind margin of AD. Corneae absent; 1 pore at posterior end. PD 190–210μ long, 110–120μ wide, separated from AD by a distance of about 12μ, rather ovoid, with truncate, slightly convex anterior margin, the widest portion about ⅔ length of plate from anterior end. Conchoidal panelling covering usually only the postero-lateral margins, but occasionally more extensive. A pair of setae at widest portion of plate and a second pair at the posterior end dorsal to the projecting anus. In the striated membranous areas of the dorsal side are 3 pairs of platelets, each bearing a seta.

AE 100μ long, convex posteriorly, with 3 pairs of setae; panelling absent. GA 142μ long, 91μ wide, oval in outline, with a deep furrow between genital and anal portions. Genital opening 55μ long and 35μ wide. A few conchoidal panels at margin of plate opposite genital opening; remainder of plate smooth, with 2 pairs of setae present. PE with a long seta dorsally, anterior to III; 2 pairs of small setae ventrally. Panels few in number, conchoidal in form and irregularly disposed. Dorsal margin of PE often very irregular between III and IV.

Capitulum 83μ long and 58μ wide; cuticle punctate but not panelled. Rostrum alone 38μ long, usually reaching to a point about ¼ length of P-2 from distal end of that segment (in one specimen it extended slightly beyond the tip of P-2); base swollen but not constricted. A series of five specimens had rostra 35 to 45μ long and 1.62 to 1.76 times as long as broad. Pharyngeal plate with 10 or 12 cells in a double row, sometimes irregular in arrangement and with open lateral cells. Palpi with P-2 somewhat swollen; P-4 much shorter than P-2; all segments faintly punctate. One long seta dorsally on P-2, 3 on basal portion of P-4 and an extremely small seta near tip of P-4. At least 1 and probably 2 setae lie closely appressed to end of P-4, but exact structure of tip of palp difficult to determine. Dorsal lengths of P-1 to P-4/vertical height: 9/27, 41/21, 14/13, 24/6μ. The spine on P-3 is very heavy and is about 8μ long and 4μ wide at base.

Chaetotaxy of legs:

	I				*II*				*III*				*IV*			
	d.	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*
1.	–	–	–	1	–	–	–	1	–	–	–	1	–	–	–	–
2.	1	1	–	–	1	1	–	–	1	–	–	1	1	1	–	–
3.	3	1	–	–	3	1	–	–	2	–	–	–	2	–	–	–
4.	3	2	–	–	3	2	–	–	2	–	1	–	2	1	–	–
5.	5	6	–	–	4	2	–	–	3	3	–	–	3	3	–	–
6.	3	2	–	1	3	–	–	–	3	–	–	–	3	–	–	–

Typically there are three setae dorsally on I-3, but frequently there are only two, the basal seta usually being the one to drop out, although at least one case was observed in which the medial member of the distal pair is absent. Medial member of ventral pair of setae on I-4 often pectinate (oil immersion); lateral member smooth. I-5 with basal pair of setae spiniform but others slender. One specimen has II-5 of both sides with two pairs of spines and two pairs of setae, but this is probably an individual variation which would be found to intergrade with the normal condition if a large enough series were available for study. In all other respects this mite is similar to the others. Outer members of 2 distal pairs of setae somewhat heavier than inner members. In addition to the setae noted in the table, I-6 bears a bacillum, a degenerate prebacillum and the divaricate parambulacral setae. Bacillum on inner surface of lateral membrane of claw fossa, and somewhat thicker distally than basally. Just anterior to the base of the bacillum is the prebacillum. In Fig. 185 the medial membrane of the claw fossa partly conceals the prebacillum and the base of the bacillum. The lateral parambulacral setae are larger than the medial setae. The abnormally erect position of the medial parambulacral seta, and also the dorsal setae in Fig. 185 is due to distortion during preparation. Medial seta of I-6 spine-like. Claws with accessory tooth but without comb. Claw fossa well developed. Median claw bidentate.

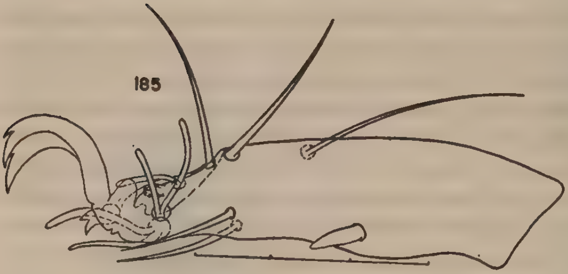
Leg II differing from I in several respects. Medial member of ventral pair of setae on II-4 extremely fine but not pectinate. II-5 with only 2 setae ventrally, the lateral one pectinate; one specimen from New Brunswick had 2 pectinate setae and 1 smooth seta ventrally on II-5 of the left side, but the right leg was normal. II-6 with no ventral setae; in addition to the dorsal setae there is a bacillum but no prebacillum, and the parambulacral seta is reduced to a single member on each side. However, there is no doubt that this represents the double seta on I-5. The bacillum is on the medial membrane rather than the lateral and is larger than that on I-6. Claws with accessory tooth and a comb, the proximal teeth usually very heavy (Fig. 183). Median claw not bidentate.

Ventro-medial setae on III-5 and IV-5 prominently pectinate, the ventro-lateral seta slender, smooth. III-6 and IV-6 with 3 dorsal setae and in addition, 2 setae near base of ambulacrum which are homologous with the divaricate setae on I-6 and their single-membered homologues on II-6. However, these setae have undergone further modification, for although the medial member is rod-like as on I and II, the lateral member is very slender and tapering. Claws on III and IV identical in form with those of II; median claw with a single tooth. In a female with a body length of 346μ the following measurements were obtained (dorsal length in μ/maximum height):

	1+2	*3*	*4*	*5*	*6*	*Ambul.*	*Total*	*T/BL*
I	35	78/28	46/27	78/23	56/13	16	309	.89
II	32	55/23	32/20	55/20	53/13	20	247	.72
III	58	50/20	35/18	66/17	70/13	22	301	.87
IV	60	61/18	37/18	66/18	65/13	20	309	.89

The color of the mid-gut is highly variable. Brown is common, but yellow and red also occur.

Male. The bodies of three males measure 291–298μ long and 148–152μ wide, L/W = 1.91–1.97. Virtually identical with female in all respects except in characteristics of GA. In a male with a body length of 291μ, GA was 150 x 107μ; the genital opening was 48 x 30μ. Genital portion of plate separated from anal portion by a deep furrow, bearing 35 to 38 setae on each side of opening. Genital opening guarded by 5 pairs of setae as shown in Fig. 184, with 3 pairs of internal genital suckers present at posterior end of opening. Panelling absent on anterior half of GA but faintly developed in raised posterior half in which genital opening is located.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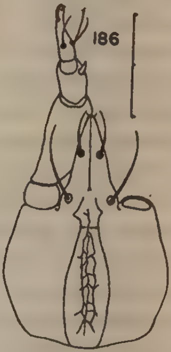
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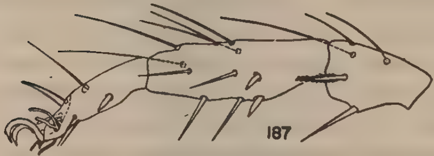
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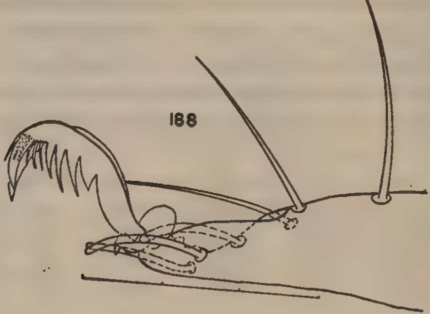
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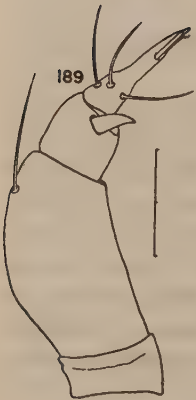
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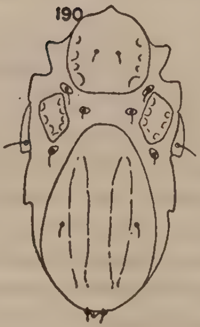
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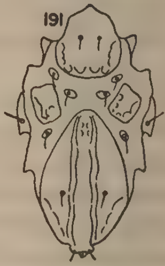
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Deutonymph. 250–260μ long, 130–140μ wide, resembling adult and protonymph in most major features (Fig. 190). I-5 with 2 pairs of setae ventrally and 4 setae dorsally. GA undivided; 2 pairs of suckers present (Fig. 182). In addition to the 2 pairs of large setae there are 2 pairs of very minute setae just anterior to the genital suckers (oil immersion).

Protonymph. The specimen from which the figure is drawn is 200μ long and 110μ wide. Closely resembling adult and deutonymph in the presence of the antero-median projection of AD, the six dorsal platelets lying in the striated membranous area and in chaetotaxy of plates. The platelets are as large as in the adult and consequently they are relatively more conspicuous. Plates prominently sculptured. PD with a pair of longitudinal costae. GA undivided, with one pair of genital suckers. I-5 with single pair of setae ventrally and the triangle setae dorsally.

Distribution. North America: St. Andrews, New Brunswick; New Haven County, Connecticut (Double Beach, Morris Cove, West River).

Baltic Sea.

Halacarus (*Thalassarachna*) *capuzinus* Lohmann and *H.* (*Th.*) *procerus* Viets 1927

These have the following characteristics in common (among others): Male and female with 3 pairs of platelets within dorsal membranous area, one between OC and AD, one between OC and OC and one between OC and PD. Each platelet bears a seta. OC without corneae.

The European forms have been separated on the following characters by Viets (1927a: 127–128).

H. capuzinus Lohmann: I-5 with 3 pairs of setae ventrally, 5 of the 6 being spiniform. AD with frontal process. Ocular plates distinctly less than twice as long as broad. Body 280–300μ long.

H. procerus Viets: I-5 with 4 pairs of ventral setae, of which the proximal pair is spine-like, the remainder setiform. OC more than twice as long as broad (67 x 30μ). Membrane between dorsal plates

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Figures 185–191. *Halacarus* (*Thalassarachna*) *capuzinus* (continued). *185* Female: I–6, median view. *186* Capitulum, ventral view. *187* Female: leg I, ventro-median view. *188* Female: II-6, lateral view. *189* Female: palp, median view. *190* Deutonymph: dorsum (same scale as *181*). *191* Protonymph: dorsum (same scale as *181*).

essentially broader than in *capuzinus.* Body 475μ long and 240μ wide. I-5 with 2 setae behind triangle setae. Rostrum 65 x 35μ (L/W = 1.86), reaching to end of P-2. AD lacking frontal process. P-2 (*not* nearly 4) 3 times as long as P-3. Membranous areas more extensive than in *H. capuzinus.* I-4 (*not*) relatively longer than in *H. capuzinus.* The parentheses have been inserted by the present writer to show where Viets' statements are refuted by his measurements or figures.

Further study of *H. capuzinus* by Schulz and by the present writer indicate that the actual differences between that species and *H. procerus* are not so great as would appear from the published descriptions, and that at least *H. capuzinus* is highly variable. Schulz (1933: 98–99) recorded a form from the Baltic which he identified as *H. capuzinus,* although it differed from Lohmann's description in a few respects. In Schulz's form I-5 had three pairs of setae ventrally, of which the basal pair was spine-like and the others setiform. This is the condition found in New Brunswick and Connecticut specimens and is probably typical of the species. That this character can be extremely variable is shown by the specimen noted by the writer in which there are four pairs of setae on I-5, of which the two basal pairs are spine-like. Another specimen shows this condition on one side of I-5 of one leg, but the other side of this segment is normal, and I-5 of the opposite leg is also normal. Another specimen has two setae dorsally and one pair of setae ventrally (Slide 43-123-62) on I-5 of the left side, but the right side is normal. It seems very probable that much of this variation is brought about by injury of the trichogens in the nymphal stages. The fact that *H.* (*Th.*) *subterraneus* shows similar variability suggests that arenicolous mites in general, especially the larger ones, may be subject to marked variations in the setae of the legs, possibly owing to the rather precarious nature of the habitat of those individuals living in the top few centimeters of the beach. In Schulz's specimens there were five setae dorsally on I-5 (as in the North American forms), whereas Lohmann noted only three.

Schulz also noted that OC is not always rhombic but may be longer, approaching those of *H. procerus* in proportions. The writer has found that in the North American forms OC may be 2.0 times as long as broad (51 x 25μ), although as a rule they are relatively shorter. The greater extent of the membranous area, the dorsal body length (475μ) and the relatively greater extent of the rostrum in *H. procerus* may be significant characters, but the differences in form between the rostrum of *H. procerus* and that of *H. capuzinus* is probably not as clear-cut as one would expect from the descriptions. In *procerus*, the rostrum is 1.86 times as long as broad (1 specimen apparently), while in the five North American specimens measured by the writer the rostrum is 1.62 to 1.76 times as long as broad. Thus, the range in these five specimens is greater than the difference between the most slender rostrum in the series and Viets' single record.

Viets (1927a: 128) gave the dorsal lengths of P-1 to P-4 as 15, 65, 22, and 37μ which agreed with his figure and scale on p. 127. But he also said (in comparing *H. capuzinus* and *H. procerus*), "Das P. II ist, mit dem des *H. capuzinus* verglichen, erheblich schlanker (fast viermal so lang wie P. III, dort wenig mehr als dreimal so lang)." This statement does not agree in any way with his measurements and is incorrect as given. According to his measurements P-2 is 2.95 times as long as P-3. In the *capuzinus* specimen measured by the writer P-2 is 2.93 times as long as P-3; that is, it is identical with Viets' *procerus* specimen. Viets' distinction based on the presumed relatively greater length of I-4 in *H. procerus* also breaks down. Using Viets' measurements for *procerus* and the writer's measurements for *capuzinus*, I-4 is 0.59 times as long as I-3 in both cases; in *H. capuzinus* I-4 is also 0.59 times as long as I-5, whereas Viets' figures of 68μ and 112μ give a ratio of 0.61, an insignificant difference. Further, two *capuzinus* specimens have been found by the writer in which the frontal process is absent, and another in which the process is so broad as to make AD appear gently rounded along the anterior margin.

Therefore, the only distinctions between *H. procerus* and *H. capuzinus* which have not been found to intergrade are the size, the extent of the membranous areas, and the proportions of OC and of the rostrum. Since Viets' description of *procerus* appears to have been based on limited material (perhaps a single specimen), it is very probable that further study will show the differences to be even less significant. Those which now exist may be attributable to the difference in size alone. Unless further work does show *procerus* and *capuzinus* to be distinct, it would be advisable to consider *procerus* a synonym of *capuzinus*. For the present, however, it seems advisable to leave the nomenclature as little disturbed as possible.

Halacarus (*Thalassarachna*) *longipes* (Trouessart) 1888

Figures 192–196

Trouessart 1888a, 755: *Leptopsalis longipes*, new species. Giard 1888, 512: *Leptosalis longipes*. Lohmann 1889a, 285–286, 292, 295–297, 302–303, 315, 317, 334–336, 338–339, 343–345, *etc.*: *Halacarus murrayi*, new species. Trouessart 1889d, 1180: *Halacarus murrayi; Halacarus levipes*, new species. Trouessart 1889a, 244–245: *Halacarus* (*Leptopsalis*) *longipes* Trt. Trouessart 1889e, 162: *Halacarus levipes*, new species. Trouessart 1894a, 155–161, 164–167, 170–171: *Halacarus murrayi* Lohm. Lohmann 1901a, 291, 293–294: *Halacarus* (*Halacarus*) *longipes* (Trouessart) 1888. Viets 1927a, 120, 125–126, 152–153, 156, 166, 168–171: *Halacarellus longipes* (Trouessart) 1888. Viets 1927b, 8, 17–18, 20–21, 34, 36–37, 47, 49, 52–55, 66: *Halacarellus longipes* (Trt.) 1888. Viets 1940g, 11, 103: *Halacarellus longipes* (Trt.) 1888.

Male. Only one adult male was taken, so that a satisfactory description of the species is not possible. It was very soft-bodied and apparently young. Body 410μ long to tips of anal papilla and 305μ wide. AD 101μ long, 102μ wide, OC 55μ long, PD 174 x 115μ. Panelling very feebly developed on PD and AD. AD and OC with a few coarse pores as shown in Fig. 196; 2 feebly developed corneae present, the posterior one much smaller than the anterior; PD with a single pair of setae. Several prominent apodemes at posterior end of AD.

AE with several delicate multi-pronged apodemes (internal); 3 pairs of setae present. PE with only 2 pairs of setae, the middle pair lying free in the membranous area on a minute sclerite. GA (Fig. 194) with an outer and an inner area in which the structure of the cuticle is slightly different. Outer portion with a structure very similar to that of the other ventral plates (thin, colorless, smooth), the inner portion faintly pigmented and thicker, bearing 90–100 (49 + 48 in the male studied) setae, the posterior setae very long. Genital opening immediately surrounded by a thick, chitinous band of unusual form and guarded by 4 pairs of spine-like setae, which are apparently internal. Two pairs of pores lie lateral to anal papilla. The anal

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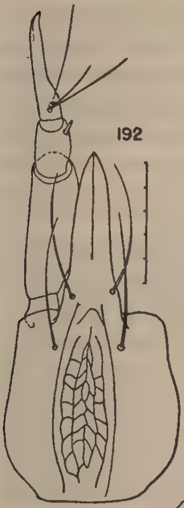
Figures 192–196. *Halacarus* (*Thalassarachna*) *longipes* (Trouessart) 1888. *192* Male: capitulum, ventral view. *193* Male: I-6, lateral view (all setae of medial side omitted, except the medial disti-dorsal seta). *194* Male: genito-anal plate. *195* Young male: venter (same scale as *196*). *196* Young male: dorsum (OC of right side obscured).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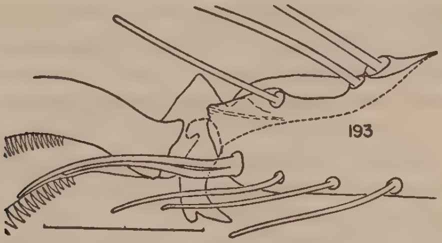
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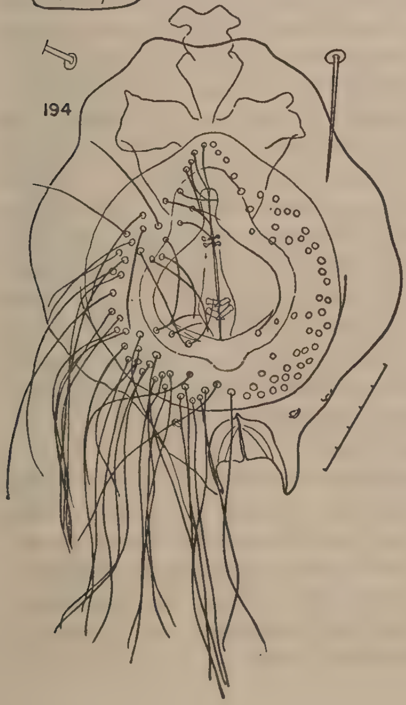
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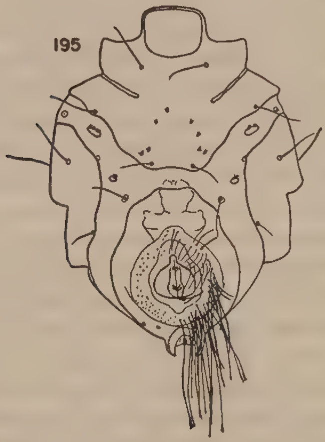
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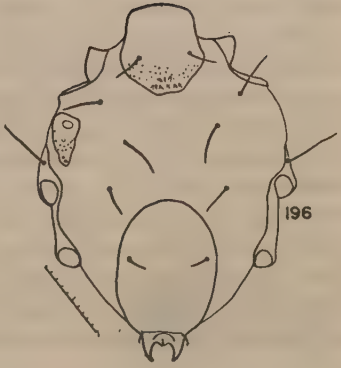
196

opercula, which are usually cusp-like in this genus, are greatly reduced, are not pointed at the end and reach only halfway to the end of the papilla. At the same time the side portions are relatively larger than usual, producing the forcipate appearance of the anal papilla which is so characteristic of this species. Membranous areas striate, with 2 pairs of apodeme-bearing platelets and a pair of minute, ring-like refractile bodies near the lateral margin between AE and PE, these probably being pores.

Capitulum (Fig. 192) 144μ long to tip of rostrum and 73μ wide; rostrum alone 71μ long and 28μ wide at base. Base of capitulum only slightly swollen. Rostrum nearly parallel-sided, the sides converging at an angle of less than 10° at the middle (therefore not strictly parallel). Tip of rostrum reaching to middle of P-3. Base of rostrum slightly swollen and bearing a pair of setae; base of capitulum bearing the second pair. Pharyngeal plate with 4 rows of closed cells.

On I-5 of the single male specimen available there are only 3 of the long setae ventrally but 4 medially (3½ pairs). In addition there are only 7 other setae on I-5 whereas Viets (1927a: fig. 49) showed 4 pairs of ventral setae plus 9 additional setae. In the specimen in the writer's collection there are 4 setae dorsally on I-3, whereas Viets showed 5. However, this is not sufficient grounds for a subspecific distinction on the basis of our present knowledge. Viets' specimen was a female, in which I-3 and I-5 measured 160 and 156μ respectively. In the author's single male I-3 and I-5 measure 121 and 119μ. The smaller number of setae in the latter may be directly correlated with this appreciable difference in size. Viets (1927b: 37) gave three additional figures of I-5. These agree with his previous figure (4 pairs of ventral setae plus 9 others). A large number of specimens from several localities would have to be examined in order to evaluate the significance of the differences pointed out above. Since, on other characters, the specimens in the author's collection are clearly *H. longipes*, it is advisable not to propose a new name.

Protonymph. This is the stage commonly taken in summer collections (from which the adults are absent). In life, they can be easily distinguished by their thick, leathery cuticle and bluish tint, as well as by the forcipate anal papilla. I-5 with 2 pairs of setae ventrally. Two pairs of corneae present on OC, the posterior one not so well developed. AD and PD small, but each contains a pair of setae (in addition to the ones just above the anal papilla).

Distribution. North America: Casco Bay, Maine; Connecticut (Stratford Point, and two unidentified stations in Long Island Sound, all below the intertidal zone).

English Channel, North Sea, Baltic, Mediterranean (?).

Genus *Copidognathus* Trouessart 1888

Trouessart 1888a, 754, 755: *Copidognathus*, new genus. Lohmann 1893a, 67–69, 75–82: "*Rhodostigma*-Gruppe." Trouessart 1893d, 259: "Section des *Rhodostigma.*" Trouessart, Neumann, 1893e, 208: "groupe *Rhodostigma.*" Trouessart 1894a, 157–158, 171–173: *Copidognathus* Trt. 1888 (emend., 1893). Trouessart 1896c, 338: "groupe *Fabricii.*" Lohmann 1901a, 286, 294, 333: *Copidognathus* Trt. 1888. Lohmann 1907a, 371, 390: *Werthella*, new genus. Trouessart 1914a, 11–12: "Groupe *Oculatus.*" Viets 1927a, 85, 87, 90–91, 134–148, 158–164, 166–168: *Copidognathus* s. str. Trt. 1888; 87, 91, 144: *Copidognathopsis*, new subgenus. Viets 1940g, 15–52, 110: *Copidognathus* s. str. Trt. 1888; 15–62, 114, 122: *Copidognathopsis* Viets 1927. Newell 1945a, 58–59: *Copidognathus* Trt. 1888.

All the "groups," genera and subgenera listed above are synonyms of *Copidognathus* s. str. because the species that are "typical" of them, or their types, are consubgeneric with *Copidognathus* (s. str.) *glyptoderma* Trouessart 1888.

Diagnosis. Palpi attached to capitulum laterally; bases of palpi separated by a distance considerably greater than width of P-1, and clearly visible in ventral view. Palpi distinctly 4-segmented. P-4 usually longer than P-2, slender, tapering; attenuate distal portion longer than basal portion. P-2 with a single, usually long dorsal seta. P-3 without setae; P-4 with 3 setae on the thick basal portion. Palpi distinctly geniculate (see key). Genital suckers internal. Predaceous, usually marine; rarely fresh water. Cosmopolitan.

Type. *C. glyptoderma* Trouessart 1888.

KEY TO NORTH AMERICAN SPECIES (MALES AND FEMALES)[21]

1a. Costae of PD with porose panels (Figs. 286, 292); not with rosette pores or modifications of these.

2a. OC drawn out into a caudiform appendage which reaches beyond insertion of leg III (Fig. 291). Female (and male?) with all ventral plates fused. With 2 pairs of maxillary setae................*bonairensis* (Viets) 1936; p. 172.
Florida; Bonaire.

2b. OC rounded or angular posteriorly, not reaching to insertion of leg III. All ventral plates separate. With 3 pairs of maxillary setae.

3a. Ocular plates less than twice as long as broad. Posterior and anterior groups of porose panels of AD not confluent (Fig. 280). Portions of dorsal plates outside porose areas very distinctly panelled. When naturally extended, leg I is at least 0.7 as long as body........*pulcher* (Lohmann) 1893; p. 167.
Florida; Bermudas, Ascension Island, Australia.

3b. Ocular plates more than twice as long as broad. Posterior and anterior groups of porose panels confluent (Fig. 284). Portions of dorsal plates outside porose areas very faintly panelled, appearing almost smooth at low magnification. Legs very short, leg I less than 0.6 as long as body.
pachypus, new species; p. 170.
Florida.

1b. Costae of PD with rosette pores (Figs. 234, 240, 248). If the rosette pores are modified, the modification consists of a reduction or loss of the canaliculi so that only a single to double row of coarse ostia or alveoli may be visible (*Copidognathus bairdi*, Fig. 234), but these never form porose panels.

4a. PD with rosette pores only on the costae (Fig. 263).

5a. Setae of AD behind posterior group (or groups) of rosette pores (Fig. 268).

6a. Costae of PD very narrow, only 1 rosette pore wide (Fig. 266). Cuticle between costae panelled, the panels not subdivided. III-6 and IV-6 with 4 setae dorsally. Leg I very nearly as long as, or as long, as body.
hummelincki (Viets) 1936; p. 162.
Florida; Bonaire; Aruba.

6b. Costae of PD 1 to 2 rosette pores wide (Fig. 268). Cuticle between costae panelled, the panels subdivided. III-6 with 4 setae dorsally, IV-6 with only 3. Leg I only about 0.8 as long as body when naturally extended.
caudatus, new species; p. 164.
Florida.

5b. Setae of AD in front of posterior group (or groups) of rosette pores (Fig. 253).

7a. AD with only 2 groups of rosette pores, the posterior group rectangular in form. Ocular plates with a sharp antero-lateral process. Corneae

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[21] Note: This key cannot be used safely to identify specimens mounted in balsam, damar, Clarite, glycerine jelly, or Berlese mixtures, because the structure of the rosette pores and certain other minute features cannot be resolved with ordinary optics when these media are employed. Hyrax, glycerine, water, and alcohol are satisfactory.

either absent, or directed forward in such a manner that they are not easily seen in dorsal view. AE with a few rosette pores behind the epimeral pores (Fig. 254).............*gracilis* (Viets) 1936; p. 160.
Florida; Curaçao.

7b. AD with 3 groups of rosette pores. Ocular plates without sharp antero-lateral process. Cornea in usual position, clearly visible in dorsal view. AE without rosette pores behind the epimeral pore (Fig. 247).

8a. OC rounded posteriorly, extending only to level of leg III, not attenuate (Fig. 245). Rostrum reaching to end of P-2. Legs I and II with well developed lamellae on segments 3, 4 and 5 (degree of variability not yet known). Costae of PD not joined posteriorly by a transverse band of rosette pores....*angustus floridensis*, new subspecies; p. 155.
Florida.

8b. OC attenuate posteriorly, extending well beyond level of leg III (Fig. 253). Legs I and II (also III and IV) with only small, usually pointed lamellae on segments 3, 4 and 5. Costae of PD usually joined posteriorly by a transverse band of rosette pores
septentrionalis (Halbert) 1915; p. 158.
Long Island Sound; Ireland.

4b. PD with a shorter band of rosette pores near each side of plate, in addition to those on costae. Each of the 4 bands may be from 1 to 4 pores wide (Fig. 197).

9a. Costae with a pronounced lateral swelling just behind level of leg IV, where the costae are about twice their normal width (Fig. 228). Rosette pores lacking canaliculi, appearing as coarse, simple pores. Female with ventral plate separate, male with ventral plates fused...*bairdi*, new species; p. 145.
Florida.

9b. Costae of relatively uniform width throughout, although sometimes slightly swollen at posterior extremities. Canaliculi present.

10a. Second pair of dorsal setae lying in the membranous area between AD and OC (Fig. 237). OC attenuate posteriorly, reaching beyond level of leg III. Posterior porose areas of AD about three times as long as broad, and lying on a W-shaped elevated portion of the plate. I-5 and II-5 with 2 sharp ventral processes (not setae).
biscayneus, new species; p. 151.
Florida.

10b. No setae in membranous area between AD and OC, the second pair of dorsal setae lying in OC near antero-median margin. Posterior porose areas of AD only 1.5 to 2.0 times as long as broad, each lying on a separate oval area of AD. I-5 and II-5 with or without ventral process.

11a. I-5 and II-5 with a pair of sharp ventral processes (not setae) as shown in Fig. 208. Lateral claws with a well developed comb, readily visible at magnifications of 400–500 x. Accessory tooth well developed. III-6 with 4 setae dorsally; IV-6 with 3.
punctatissimus (Gimbel) 1919; p. 43.
Rhode Island to North Carolina.

11b. I-5 and II-5 without a pair of sharp ventral processes. Comb very weakly developed or absent, or, if present, then visible only at highest magnifications (900–1500 x). Accessory tooth present or absent. III-6 and IV-6 each with 4 setae dorsally.

12a. Rosette pores of typical form (Figs. 205, 206), with alveolus and ostium well developed. Porose panels of AE with pores uniformly distributed over surface of panel (Fig. 223). Anterior margin of PD somewhat pointed. Rostrum not reaching to end of P-2.
acutus, new species; p. 140.
North Carolina.

12b. Rosette pores consisting essentially of depressed porose panels in which the canaliculi are restricted to the periphery of the panel; ostium of same diameter as alveolus, so that a discrete alveolus is lacking. Porose panels of AE also with pores restricted to periphery (Fig. 235). Anterior margin of PD broadly rounded or truncate. Rostrum reaching to or beyond end of P-3.
curassaviensis Viets 1936; p. 150.
Florida; Curaçao.

Trouessart's descriptions (1893d: 259–262; 1895a: 193–197, 199) of *H. poucheti* do not allow precise disposition of that species in the above key. Assuming his figures to be essentially correct, and also making certain assumptions concerning the characters of Trouessart's species which seem to be warranted by its general facies, it would fall under group 8 in the above key. It differs from *C. angustus floridensis* in its range (Spitzbergen; Labrador) and the confluent bands of rosette pores, and from *C. septentrionalis* in the possession of ocular plates which are rounded posteriorly. However, its position is by no means certain.

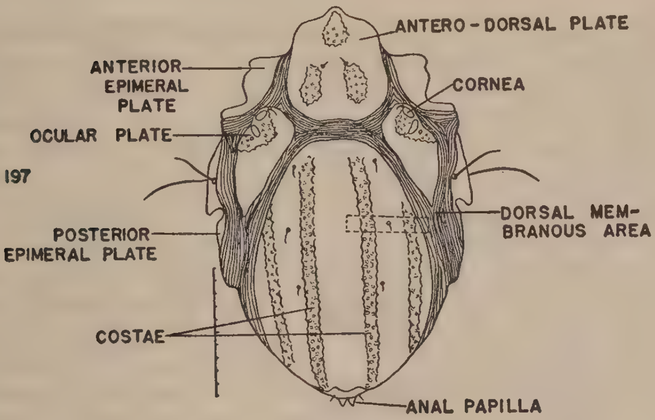
Copidognathus (s. str.) *punctatissimus* (Gimbel) 1919

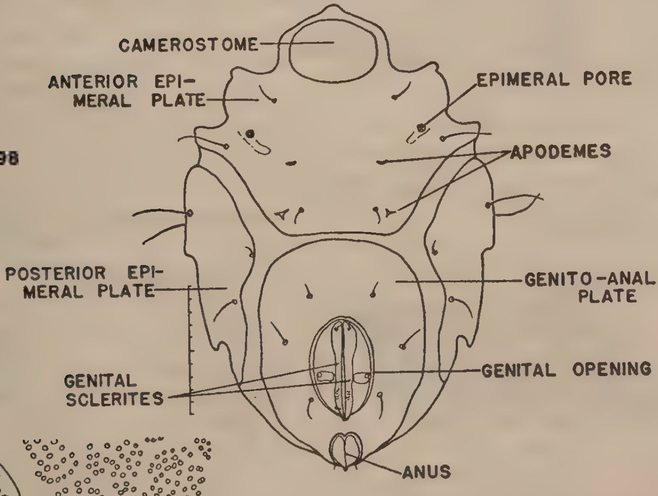
Figures 197–211

Gimbel 1919a, 106, 124–128, 130: *Halacarus* (*Copidognathus*) *punctatissimus*, new species. Viets 1928c, 79: *Copidognathus punctatissimus*.

Male. Body 318–346μ long to tip of frontal process of AD, 208–229μ wide, L/W = 1.42–1.61 (average of 5 specimens 331.0 × 217.5μ, L/W = 1.52).

Figures 197–201. *Copidognathus* (s. str.) *punctatissimus* (Gimbel) 1919. *197* Male: dorsum (rectangle shows area drawn in *200*). *198* Female: venter. *199* Female: portion of AE including the epimeral pore and a number of porose panels. *200* Female: panelling of PD (area drawn is shown by rectangle in *197*; same scale as *199*). *201* Male: palp, lateral view.


197
ANTERO-DORSAL PLATE
ANTERIOR EPIMERAL PLATE
CORNEA
OCULAR PLATE
DORSAL MEMBRANOUS AREA
POSTERIOR EPIMERAL PLATE
COSTAE
ANAL PAPILLA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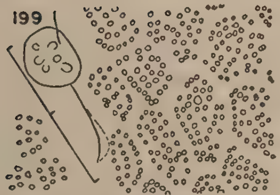
CAMEROSTOME
ANTERIOR EPIMERAL PLATE
EPIMERAL PORE
APODEMES
POSTERIOR EPIMERAL PLATE
GENITO-ANAL PLATE
GENITAL OPENING
GENITAL SCLERITES
ANUS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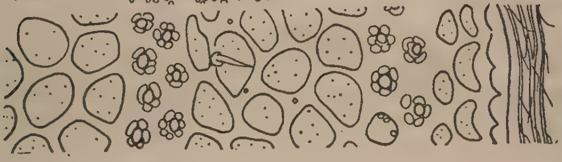
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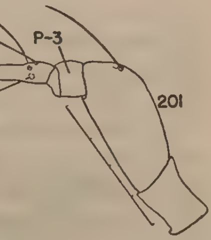
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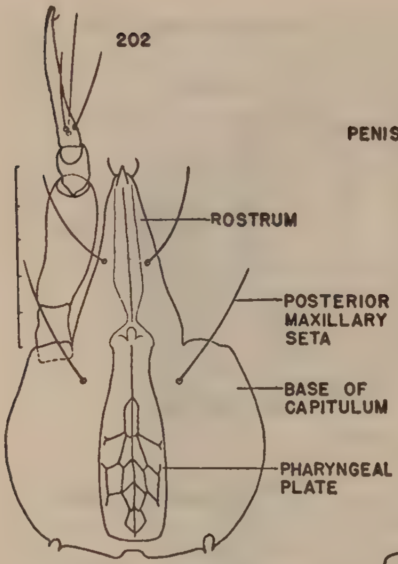
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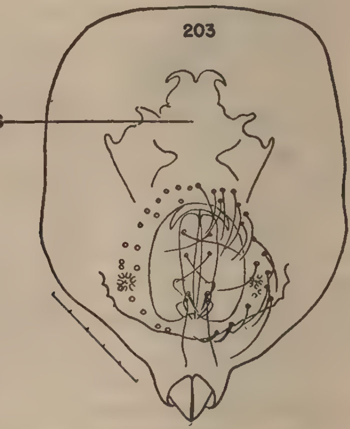
ROSTRUM
POSTERIOR MAXILLARY SETA
BASE OF CAPITULUM
PHARYNGEAL PLATE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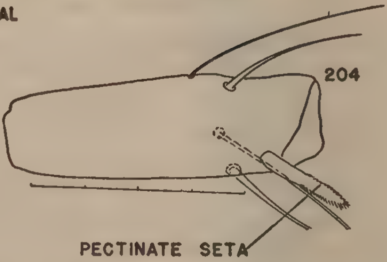
PENIS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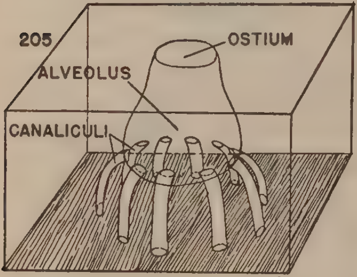
PECTINATE SETA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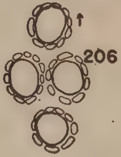
OSTIUM
ALVEOLUS
CANALICULI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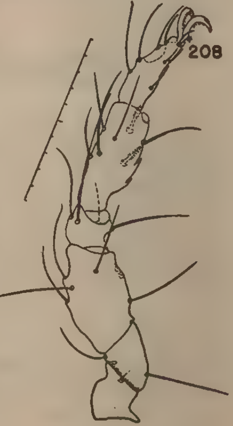
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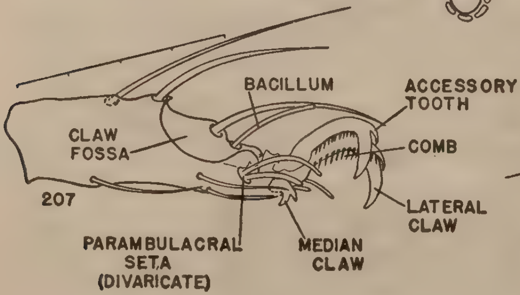
BACILLUM
ACCESSORY TOOTH
CLAW FOSSA
COMB
207
LATERAL CLAW
PARAMBULACRAL SETA (DIVARICATE)
MEDIAN CLAW

AD with a small, rounded projection just above base of capitulum; postero-lateral margins broadly rounded; posterior margin slightly concave. Panelling very well developed; 3 areas of elaborate rosette pores, with the rosettes larger and more perfectly formed than those in PD. A single pair of setae present. OC with anterior half rectangular, posterior half triangular; longitudinal axes converging anteriorly. Two corneae present, with a small area of rosette pores between them. Corneae sometimes joined by a bridge consisting of a narrow polished area at lateral ends of corneae. Posterior end of OC extending very slightly beyond insertion of leg III and tapering to a sharp point; a pair of setae at anterior end of plate. PD oval in outline, somewhat truncate anteriorly. Panelling well developed; 4 rows of rosette pores present, with the rosettes most perfectly developed in posterior half of each band. As can be seen in Fig. 200, the cuticular canals are greatly reduced in size and number as compared with those on the ventral plates (Fig. 199). The panelling effect on the dorsal plates is due entirely to the presence of depressed areas, whereas that on the ventral plates is due to a great extent to the localization of the coarse cuticular canals in roughly pentagonal or hexagonal areas, as well as to the existence of depressed areas. PD with 3 pairs of setae. Dorsal membranous areas moderately restricted; a thin band of striate cuticle visible between PD and anus. Membranous areas pilose, the hairs extremely fine and ranging up to 8μ in length.

Venter as in female, except for characters of GA. Genital opening extending to middle of GA, surrounded by 16 to 20 setae on each side. A group of 5 to 8 puncta on each side of opening. Opening guarded by 2 narrow sclerites bearing 4 pairs of setae. Anus projecting beyond end of body. Cuticle distinctly panelled. Capitulum and legs as in female. Palp (Fig. 201) in a male with PD 224μ long with P-1 to P-4 having following lengths: 19, 38, 10, 40μ.

Female. Body 325–360μ long to tip of frontal process, 208–249μ wide (L/W = 1.43–1.56) (average of 10 specimens, 343.5 x 226.5μ, L/W = 1.52); slightly larger than male. Dorsal and ventral surfaces as in male, except for GA. AE with 3 pairs of setae and pores as

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Figures 202–208. *Copidognathus* (s. str.) *punctatissimus* (continued). *202* Female: capitulum, ventral view. *203* Male: genito-anal plate. *204* Male: III-5, median view. *205* Schematic representation of structure of rosette pore. A portion of cuticle containing a single rosette pore has been drawn as a semitransparent object. *206* Rosette pores of left posterior porose area of AD (same scale as *200*). *207* Female: I-6, median view. *208* Male: leg I, lateral view.

shown in Fig. 198. PE with 1 pair of setae dorsally and 3 pairs ventrally, the most anterior of the ventral setae being almost completely lateral. GA with 3 pairs of setae, the genital opening guarded by a pair of slender sclerites which bear a pair of setae anteriorly. One pair of suckers is readily seen, but the others are not, although they probably are present. Anus terminal.

Capitulum (Fig. 202), in a female 356μ long, 111μ long to tip of rostrum; rostrum alone 51μ long, usually reaching to middle of P-3. Tip of rostrum very sharp; sides of rostrum converging uniformly throughout, except at very tip, and not constricted at base. Base of capitulum 73μ wide, heavily punctate except for the smooth area just ventral to pharynx; panelling not as distinct as on ventral plates. Pharyngeal plate with 5 pairs of median closed cells, and 2 pairs of lateral cells, one or both of which may be closed. Some specimens have a third pair of lateral cells anterior to those shown in Fig. 202. Palp as in male.

Chaetotaxy of legs:

	I				*II*				*III*				*IV*			
	d.	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*
1.	–	–	–	1	–	–	–	1	–	1	–	–	–	–	–	–
2.	1	1	–	–	1	1	–	–	1	1	–	–	1	1	–	–
3.	3	1	1	–	3	1	1	–	2	1	–	–	2	1	–	–
4.	2	2	–	–	2	2	–	–	1	1	1	–	2	1	–	–
5.	3	1	1	2	3	1	1	2	2	2	1	–	2	2	1	–
6.	3	3	–	–	3	–	–	–	4	–	–	–	3	–	–	–

In a male with a body length of 304μ the following measurements were obtained:

	1+2	*3*	*4*	*5*	*6*	*Ambul.*	*Total*	*T/BL*
I	42μ	65*	23	65	49	23	267	.78
II	44	58**	23	56	53	27	261	.77
III	60	48	25	60	65	28	286	.84
IV	65	58	28	60	63	28	302	.89

* Dorsal height = 38μ. ** Dorsal height = 30μ.

Legs rough-looking, thick-walled. All femora panelled, the panelling on I and II especially prominent. Basal segments, especially trochanter, pilose, the pilosity appearing principally at disti-dorsal end of segment. I-3 1.7 times as long as high (swollen) and with prominent punctate area ventrally. I-5 with 2 pectinate setae ventro-medially and a single smooth seta ventrally. Ventral margin with 2 very sharp, thin processes directed distally. I-6 with 3 large setae dorsally and 3 small setae ventrally, the latter being difficult to find except with oil immersion. There is also a bacillum on the lateral membrane of the claw fossa and a pair of divaricate parambulacral setae. The prebacillum is very rudimentary or absent, but one can usually find a minute, closed canal extending from the lumen of the tarsus toward the point where it is ordinarily found. Claw fossa very deep but almost completely open medially because of small size of medial membrane. Lateral claws weakly pectinate, with accessory tooth; median claw bidentate.

Leg II remarkably similar to I. II-3 1.90 times as long as high; II-5 identical with I-5, medial setae pectinate. II-6 identical with I-6 except for absence of the 3 ventral setae; bacillum lateral. Medial membrane of claw fossa as on I-6. Lateral and median claws as on I-6, but pecten more strongly developed. III-5 (Fig. 204) with a heavy pectinate seta medially. III-6 (Fig. 211) with 4 setae dorsally and a pair of setae at base of ambulacrum, the homologues of the divaricate setae on I and II. Medial seta of this pair rod-shaped and rounded terminally; lateral member moderately heavy, tapering and serrate. IV without the heavy pectinate setae found on III-5, but with an ordinary seta in its place (Fig. 210). IV-6 with only 3 setae dorsally and the pair at the base of the ambulacrum, both of the latter tapering and serrate (Fig. 209). In the female these are of the same form, but the serration is very feebly developed or absent. III-6 and IV-6 with a shallow fossa; membranes very low. Claw IV like III, but slightly longer.

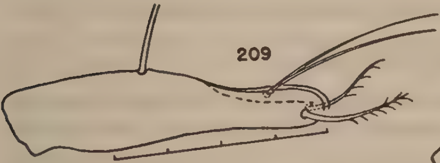
Remarks. This is unquestionably *C. punctatissimus* (Gimbel) 1919 (pp. 124–128), but there are certain differences between the description above and that given by Gimbel (based on two males and a third specimen whose sex could not be determined). The writer has had the advantage of examining many specimens from several localities. Gimbel stated that the rostrum is rounded anteriorly and reaches to the end of P-3, but in the specimens examined by the writer the tip of the rostrum is very sharply pointed, although it widens rapidly just behind the tip, and it almost invariably reaches only to the middle of P-3. Gimbel's specimens were probably somewhat compressed in preparation, as he gave L/W = 1.35, which is broader than any of the fifteen mites measured by the writer. Gimbel noted only a single pair of setae on AE, whereas there are the usual three pairs. Gimbel's "zwei Schuppen" are probably apodemes. The writer found leg IV to be distinctly longer than I, and leg II is not appreciably shorter than I. The two heavy setae which Gimbel noted only on II-5 are found also on I-5 and are distinctly pectinate on both legs (oil immersion). As careful study shows that the setae on legs I and II are identical except for the absence of the three very minute ventral setae on II-5, it may be assumed that Gimbel referred to these setae when he said: "Tastborsten befinden sich nur an dem Vorderbeinen." However, Gimbel did not figure the ventral setae of I-6 in his fig. 22a. Gimbel's specimens were slightly smaller than those observed by the writer. The type locality was given simply as Newport (North America), which was probably Newport, Rhode Island, rather than Newport News, Virginia, although the known range includes both localities. Because the rostrum is not as long as reported by Gimbel, and because I-5 and II-5 have pectinate setae, this species cannot be identified through the use of Viets' keys (1927a: 134–139; 1940g: 17–27).

Examination of specimens from Beaufort shows that the species is very constant throughout its known range. A close study of the following characters show the Beaufort mites to agree completely with the above description. Panels of PD with a few scattered puncta, and with coarser pores between the depressions (as in Fig. 200); membranous areas pilose. Setae on sclerites guarding genital opening identical in form and position with those of the northern forms. I-5 and II-5 with pectinate medial setae, and with 2 sharp processes ventrally. III-6 with 4 setae dorsally; IV-6 with only 3 setae here. Homologues of parambulacral setae as described above. Size as given above for the northern forms. All these minute characters, then, have a high degree of validity for recognition of this species throughout its known range.

Distribution. North America: Rhode Island (Newport; and 3 miles north of Block Island, at 34 meters); New Haven County, Connecticut (Morris Cove; South End; Double Beach); Beaufort, North Carolina (Piver's Island; Town Marsh; Harker's Island).

Figures 209–211. *Copidognathus* (s. str.) *punctatissimus* (continued). *209* Male: IV-6, lateral view. *210* Male: IV-5, median view. *211* Male: III-6, median view.

Figures 212–218. *Copidognathus* (s. str.) *acutus* new species. *212* Male: IV-6, median view. *213* Male: dorsum. *214* Male: genito-anal plate. *215* Male: palp, lateral view. *216* Female: venter. *217* Male: I-6, median claw. *218* Portion of right posterior group of rosette pores of AD.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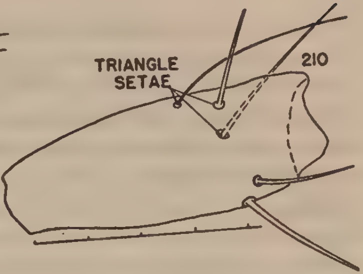
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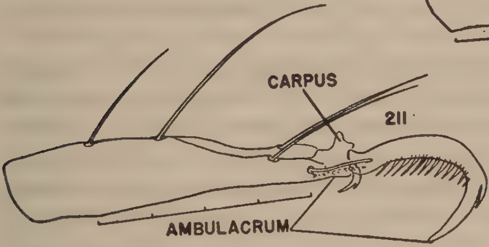
TRIANGLE
SETAE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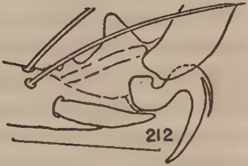
CARPUS
AMBULACRUM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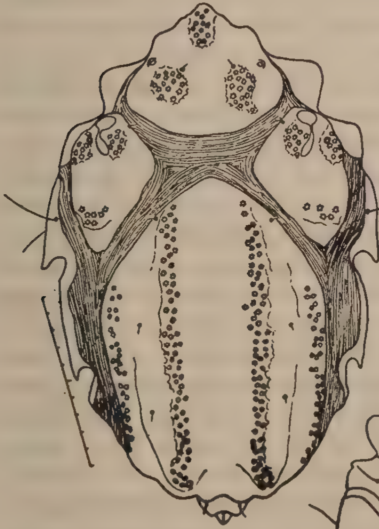
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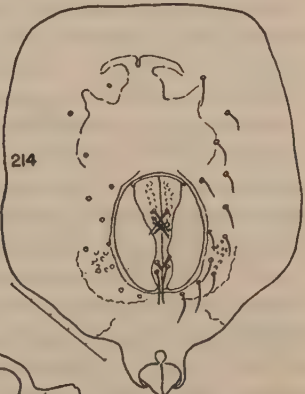
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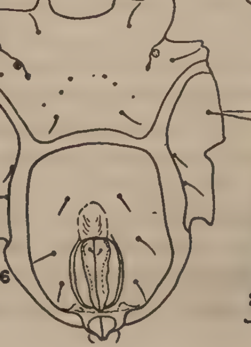
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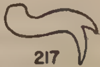
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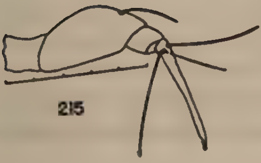
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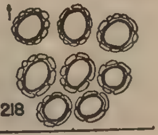
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Copidognathus (s. str.) *acutus*, new species

Figures 212–223

Male. Body 291–318μ long, 187–211μ wide, 1.48–1.59 times as long as wide; average of 8 specimens 305.5 x 200.1μ, L/W = 1.55. Superficially similar to *C. punctatissimus* (Gimbel), with which it occurred at Beaufort, North Carolina, but differing from it in many details.

In a male 305 x 198μ the following measurements were obtained: AD 91μ long, 97μ wide; each OC 91 x 56μ; PD 214 x 144μ. AD broader than long, with a frontal process of variable sharpness, with 3 prominent elevated porose areas and a pair of setae. Posterior margin broad, convex. OC broad, the antero-median margin about ⅔ as long as postero-median margin. Corneae usually joined by a bridge of refractile cuticle, the seta mediad of anterior cornea. Three areas of rosette pores present, the posterior one of which contains from 1 to 15 pores (highly variable), and has never been found absent. Posterior end of OC sharply rounded, or slightly angular, extending only to level of leg III. PD with sides nearly parallel for a considerable distance; antero-lateral margins converging rapidly (forming an angle of about 90°) to a usually sharply rounded point (hence the specific name, *acutus*). Costae prominent, with rosette pores, the posterior end turned outward; a second row of rosette pores along each side of plate, nearly continuous with the more medial row at posterior end of plate. Three pairs of setae present as shown, the anterior pair always at edge of plate, the posterior pair well behind insertions of leg IV. Dorsal plates only faintly panelled in most specimens; panels subdivided so that a faintly reticulate pattern is imposed upon the panel pattern (Fig. 222). A minute pore is visible under each subdivision of the panels, but the pores do not reach the surface in all cases. Rosette pores of AD (Fig. 218) much larger than those of PD; those on OC of the same type as found on PD, but sometimes slightly larger. In addition to the rosette pores there is a pair of large pores on AD (antero-laterally from posterior rosette areas), OC (lateral to posterior corneae), and PD (at ends of costae). However, the pore found between setae 2 and 3 in PD of *C. bairdi*, n. sp., has no homologue in *C. acutus*, n. sp. Membranous areas moderately restricted.

Ventral armor as in female except for characters of GA. In a male with a body length of 305μ the following measurements were obtained:

GA 166 x 130μ, genital opening 53 x 39μ, 71μ from anterior end of plate. Anal papilla prominent. Cuticle panelled and punctate as on AE, except around the opening where the cuticle is smooth with a few scattered minute pores. Genital opening guarded by a pair of heavy sclerites bearing 4 pairs of setae, the anterior end of each plate sculptured. An area of 7 to 10 puncta present on each side of posterior half of genital opening.

Capitulum (Fig. 220), in a male 305μ long, 86μ long to tip of rostrum, and 63μ wide; rostrum alone 41μ long and 29μ wide at base, not reaching to end of P-2. Sides of rostrum converging uniformly except at tip; not constricted at base. Base of capitulum densely porose. Palpi (in a male with a body 291μ long) with P-1 to P-4 as follows: 16, 37, 8, 44μ long; P-4 longer than P-2 (Fig. 215).

Chaetotaxy of legs:

	I				*II*				*III*				*IV*			
	d.	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*
1.	–	–	–	1	–	–	–	1	–	1	–	–	–	–	–	–
2.	1	1	–	–	1	1	–	–	1	1	–	–	1	1	–	–
3.	3	1	1	–	2	2	1	–	2	–	–	–	2	1	–	–
4.	2	2	–	–	1	1	1	1	1	1	1	–	1	1	1	–
5.	3	1	1	2	3	1	1	2	3	2	–	–	3	2	–	–
6.	3	3	–	–	3	–	–	–	4	–	–	–	4	–	–	–

In a small male with a body length of 291μ the following measurements were obtained (for I-3, I-5, II-3 and II-5 the height is also given):

	1+2	*3*	*4*	*5*	*6*	*Ambul.*	*Total*	*T/BL*
I	38μ	66/30	23	65/18	44	20	256	.88
II	35	59/25	21	53/20	48	23	239	.82
III	54	47	22	56	56	28	263	.87
rt. IV	56	56	26	58	60	30	286	.98
lt. IV	59	55	26	59	61	29	289	.99

In an appreciably larger female (exact length unknown) legs III and IV had the following measurements:

	1+2	*3*	*4*	*5*	*6*	*Ambul.*	*Total*	*T/BL*
III	56μ	49	23	58	59	27	272	?
IV	61	59	25	62	62	29	298	?

Since the legs of this specimen are not much longer than those of the male (only 3 to 4%), it is probable that if the exact length of this specimen were known, legs IV would not be 0.98 to 0.99 times as long as the body, but somewhat shorter.

I-3 (Fig. 219) 2.20 times as long as high (not swollen); dorsal setae relatively short, erect. Medial setae of I-5 pectinate (oil immersion), the distal seta larger than the proximal one. I-6 with the bacillum and parambulacral setae in addition to those noted in table; prebacillum absent. The 2 disti-ventral setae are rounded terminally like the parambulacral setae, but the basi-ventral member of this group is tapering. In one male, at a magnification of 1500 diameters, a very reduced comb is found along the inner side of claws I, III and IV (Fig. 221); but on another specimen (female) no trace of a comb is found. This presumably is not a sexual difference, but simply an individual variation. The comb never extends to the concave inner margin of the claw and would be visible only under the most favorable conditions even when present. In some specimens an extremely fine, hairlike, accessory tooth is present, but in others it is represented only by a slight break in the outline of the convex side of the claw, and in others the outer side of the claw is completely smooth. Under low magnifications the lateral claws of all specimens appear smooth, with neither accessory tooth nor comb. Median claw coarsely bidentate (Fig. 217). Claw fossa shallow, completely open medially. I-1 hirsute dorsally and lateral half of I-3 also hirsute, the hairs being longest disti-ventrally. Lateral surface of I-3 also faintly panelled; medial surface neither hirsute nor panelled.

In II-3 the dorso-lateral seta has shifted to a completely lateral position, while the homologue of the lateral seta of I-3 has become ventral. II-3 2.36 times as long as high. Medial setae of II-5 pectinate, the distal one very long, extending nearly to level of basi-dorsal seta of II-6. II-6 like I-6 except that the bacillum is twice as far from disti-dorsal seta as from base of claw, and the ventral setae are lacking. II-1 and II-3 hirsute as on leg I.

III-3 with 2 very slender setae dorsally, but none ventrally; IV-3 with 2 setae dorsally and one ventrally. III-5 with disti-ventral seta

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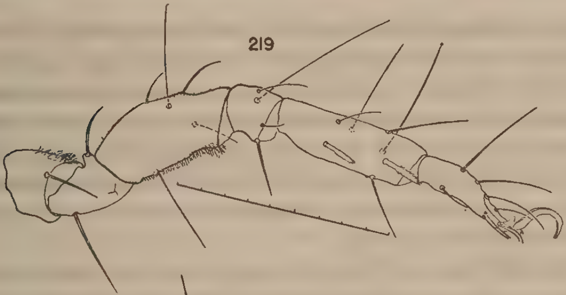
Figures 219–223. *Copidognathus* (s. str.) *acutus* (continued). *219* Male: leg I, median view (the median seta was drawn in from the opposite leg). *220* Male: capitulum, ventral view. *221* Male: III-5 and III-6, median view. *222* Female: PD, at level of second seta. *223* Male: porose panels of AE.

Figures 224–227. *Copidognathus* (s. str.) *bairdi* new species. *224* Female: genito-anal plate. *225* Male: venter. *226* Portion of left posterior porose area of AD. *227* Cross-section of femur.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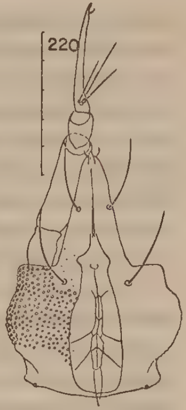
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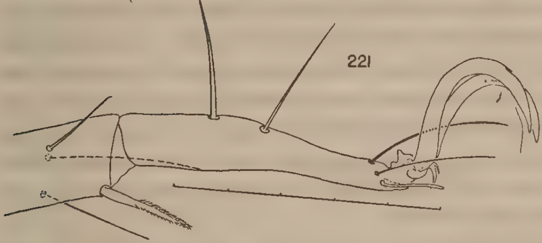
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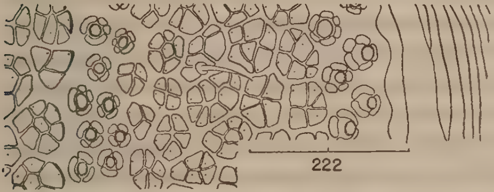
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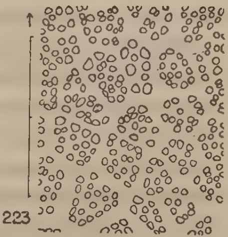
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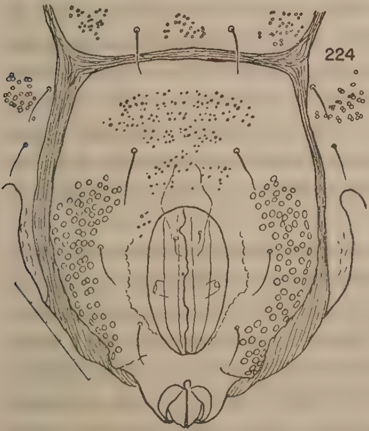
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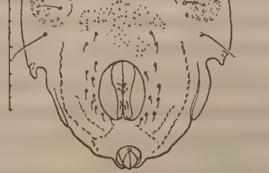
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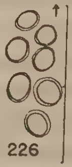
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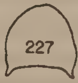
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heavy, pectinate; homologous seta on IV-5 slender, tapering. III-6 and IV-6 each with 4 setae dorsally, the basi-dorsal one on IV-6 characteristically short, blunt. On III-6 the homologues of the parambulacral setae consist of a rod-shaped seta medially and a spine-like seta laterally (Fig. 221); on IV-6 they are both spine-like (only the medial one is shown in Fig. 221). Tarsi III and IV slightly flattened disti-dorsally but without true fossa. Median claw with the 2 teeth much more slender than on I and II.

Female. Six females measure 284–319μ long, 180–211μ wide, L/W = 1.48–1.58 (average 306.8 x 201.5, L/W = 1.53); dimensions as in male. Differing from male only in characters of GA. Ventral plates prominently panelled and porose. GA with 3 pairs of setae, the genital opening very close to anus, considerably more than its own length from anterior end of GA, guarded by a pair of finely sculptured sclerites, each bearing a seta at the anterior end. In a female 315μ long, GA was 161μ long and 120μ wide; the opening was 61 x 38μ and was 76μ from anterior end of GA.

Remarks. This species goes to *C.* (s. str.) *latus* Viets 1927 in Viets' key (1927a: 134–139) and is more closely related to that species than to any other yet described. The species differ in the following respects.

C. acutus: Body 284–319μ long. Rostrum shorter than base of capitulum, not reaching to end of P-2. P-4 longer than P-2. PD including the anterior pair of setae. Posterior ends of costae diverging. Lateral rows of rosette pores extending an equal distance each way from the insertions of leg IV. OC with a group of rosette pores on the posterior half of the plate. Dorsal and ventral membranous areas relatively reduced. Female genital opening 0.38–0.39 as long as GA, but removed from anterior margin of GA by a distance 1.25 times as long as opening. PE with 3 pairs of setae ventrally. Lateral claws with feebly developed comb and accessory tooth which may often be absent. Medial setae of I-5 and II-5 pectinate. III-6 and IV-6 each with 4 setae dorsally.

C. latus: Body 505μ long. Rostrum longer than basal part of capitulum, reaching somewhat beyond end of P-2. P-4 shorter than P-2. Homologues of anterior setae of PD lying in the membranous area. Posterior ends of costae converging. Viets did not mention the lateral rows of rosette pores on PD, although he did figure them (Viets 1927a: fig. 74). However, it is not certain from Viets' drawing that he showed the full posterior extent of the lateral rows. If he did, then they are much shorter than those in *C. acutus*, for they are only half as long and end at the level of IV. OC without posterior porose area. Dorsal and ventral membranous areas relatively extensive. Female genital opening 0.40 as long as GA, but removed from anterior margin of GA by a distance only 0.75 the length of the opening. Viets showed PE as having only two pairs of setae ventrally, which is a significant character if correct. Lateral claws with a distinct comb and tooth. According to Viets the medial setae on I-5 are not pectinate, but those on II-5 are. Viets (1927a: fig. 76c) showed only three setae dorsally on III-6.

Distribution. North America: Beaufort, North Carolina (Piver's Island [type locality]; Newport River, at 2.5 meters; Harker's Island; off Beaufort Entrance, at 10 meters).

Copidognathus (s. str.) *bairdi*, new species

Figures 224–234

Male. Body 270–284μ long, 159–180μ wide, L/W = 1.57–1.69 (av. 277.0 x 142.7μ, L/W = 1.61), based on 5 males. Somewhat shorter than female and appreciably narrower. AD produced anteriorly, the posterior half sharply elevated above anterior half just anterior to middle of plate; 3 large areas of coarse pores and a pair of minute setae present; a few large pores at posterior margin. OC tapering to a sharp point just behind leg III. Two corneae, 2 porose areas, and 1 seta present on each plate. Lateral porose areas forming a prominent lateral projection. PD usually rounded anteriorly, slightly truncate or somewhat concave, the shape of this part of the margin being greatly influenced by the degree of development of costae. The latter are sharply elevated and bear a row of coarse simple pores, 1 or 2 pores wide. Behind leg IV the costae are greatly swollen laterally and bear a pair of large pores. Posterior ends of bands also slightly swollen. A single row of simple pores along each side of plate between levels of legs III and IV. Three pairs of setae present at positions shown in Fig. 228. All dorsal plates distinctly panelled, the walls of the panels usually tuberose, and the panels subdivided by smaller ridges (Fig. 234). Under oil immersion it can be seen that the ostia in the 12 porose areas of the dorsal plates open into alveoli of greater diameter, which in turn appear to continue through the cuticle. Canaliculi absent. In Fig. 228 the circles representing the pores actually represent the deeper portions of these rather than the minute external openings. Membranous areas greatly reduced. In the specimens in the writer's collection, AD overlaps OC, and sometimes PD also, which is probably due to shrinkage.

Venter (Figs. 225, 229) with plates almost completely fused. AE fused with PE, or separated from it by only a suture; fused with GA. Membranous areas completely absent. GA fused with PE. The plates carry the setae characteristic of the genus. Panelling absent except for a pair of small areas on GA at each side of posterior half of genital opening. PE with a dorso-lateral notch anterior to III and IV. GA coarsely porose, the pores of the same type as those found on PD (Fig. 234). AE with a Y-shaped porose area. In the central portion of this the pores are small and single, but at the ends of the arms and the stem of the Y the pores are larger and tend to clump together and even to coalesce (Fig. 233). A patch of single pores is also found at the anterior end of GA, and six other patches of clumped or coalesced pores as shown in Fig. 225. In all these areas the pores are of the same type as those on PD, but usually smaller. Genital opening with 10 or 11 very slender setae on each side, but without punctate areas such as are found in *C.* (s. str.) *punctatissimus*. Opening guarded by a pair of sclerites bearing 4 pairs of setae. In a male with a body length of 277µ the opening was 48 x 38µ (L/W = 1.26).

Capitulum (in a male with a body length of 277µ) 75µ to tip of rostrum and 56µ wide at base. Rostrum alone 34µ long and 22µ wide at base, not reaching to end of P-2. Setae as in Fig. 231. Base of rostrum with pores like those on PD. Dorsal wall of pharynx faintly panelled, the lateral walls of panels sometimes indistinct. Palpi and legs as in female.

Female. Body 291–305µ long, 191–201µ wide, L/W = 1.45–1.53 (av. 293.6 x 198.1µ, L/W = 1.48), based on 5 specimens, somewhat longer and appreciably wider than male. Dorsal plates as in male, but PD broader. In a female with a body length of 298µ, PD was 201 x 139µ (L/W = 1.44); whereas in the male in Fig. 228 L/W = 1.54. Ventral plates characteristic for the genus, not fused as in male; membranous areas well developed, striate. Distribution and form of pores as in male. GA nearly parallel-sided, slightly convex anteriorly (Fig. 224), with 3 pairs of setae. Genital opening guarded by a pair of sclerites bearing a single pair of setae near anterior end; a single pair of genital suckers visible. In a female with a body length of 298µ the following measurements were obtained: GA 156 x 111µ; genital opening 60 x 35µ, 63µ from anterior end of GA.

Palpi (Fig. 230) in a female with PD 205μ long, with P-1 to P-4 13.5, 36, 7.5, 41μ long. P-4 longer than P-2.

Chaetotaxy of legs:

	I				*II*				*III*				*IV*			
	d.	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*
1.	–	–	–	1	–	–	–	1	–	1	–	–	–	–	–	–
2.	1	1	–	–	1	1	–	–	1	1	–	–	1	1	–	–
3.	3	1	1	–	3	1	1	–	2	–	–	–	2	–	–	–
4.	2	2	–	–	1	1	1	1	1	1	1	–	2	1	1	–
5.	4	1	–	2	3	1	1	2	2	1	1	1	2	1	1	1
6.	3	3	–	–	3	–	–	–	4	–	–	–	4	–	–	–

In a female with a body length of 305μ the following measurements were obtained (for I-3, I-5, II-3 and II-5 the height is also given):

	1+2	*3*	*4*	*5*	*6*	*Ambul.*	*Total*	*T/BL.*
I	34μ	65/33	22	68/25	44	19	249	0.82
II	31	50/26	19	53/23	48	22	223	0.73
III	47	47	17	53	58	26	248	0.81
IV	49	52	18	53	59	25	256	0.84

I-3 and II-3 1.98 and 1.92 times as long as high (only slightly swollen). All femora with ventrally projecting carinae which make the ventral side of the segment somewhat concave (Fig. 227). Panelling feebly developed on I-3, the rest of the legs only punctate. All claws pectinate, median claw bidentate.

Leg I without ventral process on femur; 3 heavy setae ventrally and medially on I-5. In one specimen the medial setae appear pectinate, but the pectinations are so fine that they would show up only in specimens favorably oriented. I-6 almost identical with I-6 of *C. punctatissimus*, except that the bacillum is somewhat more distally placed (about halfway between disti-dorsal seta and base of claw) and is more tapering. Medial membrane of claw fossa completely lacking. Prebacillum absent. II-5 with medial setae somewhat more distinctly pectinate; II-6 identical with I-6 except for absence of 3 ventral setae. Bacillum lateral, about halfway between disti-dorsal seta and base of claw, the medial membrane absent. III-3 and IV-3 without ventral seta. III-4 with 1 seta dorsally, IV-4 with 2. III-5 as in *C. punctatissimus* (Fig. 204), with a long, smooth ventral seta and a long pectinate seta; IV-5 with pectinate seta replaced by a slender seta. III-6 and IV-6 each with 4 setae dorsally (compare with *C. punctatissimus*).

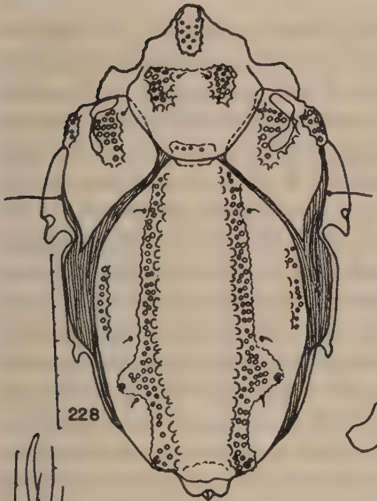
In IV-6 the most proximal of the dorsal setae is retained, whereas in *C. punctatissimus* it does not develop. At the base of the ambulacrum of III-6, on the medial side, is a rod-like seta as in *C. punctatissimus;* but it is paired with a short spine-like seta, the form of which is difficult to discern because of its close apposition to the tarsus. IV-6 with both members of this terminal pair short and spine-like. III-6 and IV-6 with shallow claw fossa, but with no distinct membranes.

Remarks. This species is very closely related to *C.* (s. str.) *gibberipes* Viets 1936 (Bonaire, Dutch West Indies). The pores at the posterior end of AD are much fewer in number (4–8) than in *C. gibberipes* (ca. 20), and the cuticle between and anterior to the posterior porose areas of AD is distinctly panelled. The lateral swellings of the costae of PD are more prominent than in *C. gibberipes*, and there is a single row of pores along each side of PD which Viets did not figure or mention in his *C. gibberipes.* Pores are entirely lacking from the remainder of PD, whereas in *C. gibberipes* there are large pores between the costae. Viets showed no lateral expansion of OC in the region of the lateral porose areas of these plates, but in *C. bairdi* this expansion is considerable. Capitulum appreciably shorter, rostrum not reaching to end of P-2; in *C. gibberipes* the rostrum reaches beyond P-3. The base of the capitulum is coarsely porose. The posterior pair of setae is borne on the base of the capitulum; but in *C. gibberipes* these are on the rostrum itself. I-3 with ventral carinae ("leicht lamellosen Beugeseitenerweiterung" of Viets 1936d: 404) but without a tubercle.

Viets' statement on page 405 "Alle Krallen haben eine kleine Aussenzinke, aber keinen Kamm" is obviously unintentional, for his figures show all claws pectinate. This error is repeated elsewhere (Viets 1940g: 26). Viets was uncertain of the sex of his mite, saying simply that it was "vermutlich ein Männchen." However, ratios calculated from Viets' measurements of PD and the genital opening are intermediate to the ratios obtained for the males and females of *C. bairdi* and are therefore inconclusive. Calculating the position of the morphological "anterior margin" of GA of the male of *C. bairdi*

Figures 228–234. *Copidognathus* (s. str.) *bairdi* (continued). *228* Male: dorsum. *229* Male: genito-anal portion of venter. *230* Female: palp, lateral view. *231* Male: capitulum, ventral view (slightly rotated). *232* Female: leg I, median view. *233* Male: portion of AE outlined by dotted lines in *225*. *234* Male: panelling and pores of PD, halfway between setae 1 and 2 (same scale as *233*).

Figures 235–236. *Copidognathus* (s. str.) *curassaviensis* Viets 1936. *235* Female: porose panels and an apodeme of AE. *236* Female: capitulum (slightly rotated).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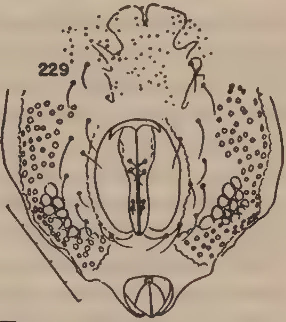
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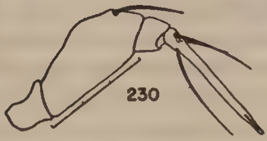
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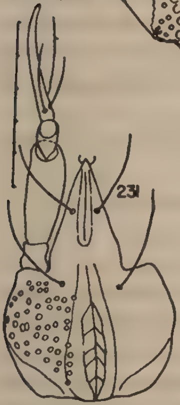
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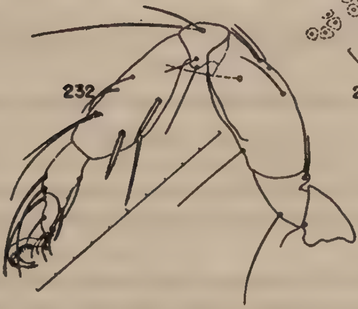
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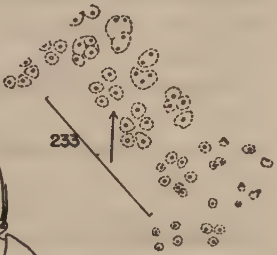
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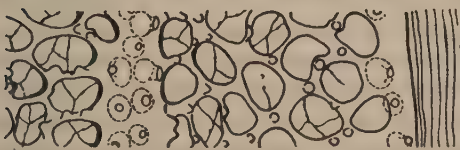
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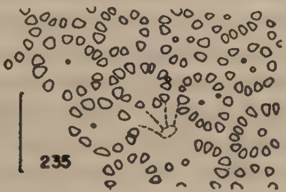
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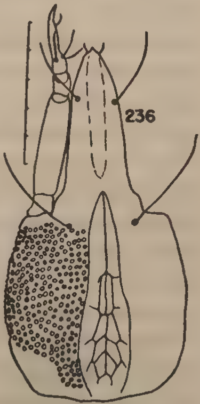
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(using the anterior setae of GA, the posterior setae of AE and the middle pair of setae of PE as reference points), the anterior margin of the plate would lie 142μ from the tip of the anal papilla. The male genital opening is 46μ long in this specimen (Fig. 225). The corresponding measurements in the female are 156μ and 60μ (see text above). Therefore, in the male of *C. bairdi* the ratio of length of GA to the length of the genital opening is 3.09; in the female it is 2.60. Viets' figures of 128μ and 54μ give a ratio of 2.37, which suggests a female rather than a male. The fact that these two species are very closely related (despite the numerous minor differences pointed out above) also suggests that Viets' mite was a female, for one would be justified in expecting that the ventral plates in the two species would correspond, and therefore that the male of *C. gibberipes* Viets 1936 would have fused ventral plates and the female separate ventral plates. Since Viets was able to measure GA and did not note any fusion (such as he noted in *C. bonairensis* [Viets] 1936: 416), it seems very probable that Viets' description of *C. gibberipes* was based on a female and not on a male.

Distribution. North America: Florida (Biscayne Bay, on Soldier's Key).

Copidognathus (s. str.) *curassaviensis* Viets 1936

Figures 235–236

Viets 1936d, 390–391, 399–402: *Copidognathus* (s. str.) *curassaviensis*, new species. Viets 1940g, 24: *Copidognathus* (s. str.) *curassaviensis* Viets 1936.

Viets (1936d: 399–402) gave a good account of this species, and the specimens in the writer's collection agree well with his description and figures. However, a very small comb is found on claws II and IV, so that one must overlook the first dichotomy in using Viets' key (1940g: 17). The presence or absence of combs on the claws of *Copidognathus* species is an undesirable primary key character, for although there are many species with clearly pectinate claws, and some which have completely smooth claws (but usually with an accessory tooth), there are many in which the comb is present but difficult to observe, even with oil immersion. In this latter group of species which are apparently in the process of losing the pecten, there are unquestionably some species which show individual variation (e. g., *C. acutus*, n. sp.), some specimens having smooth claws, and others having faintly pectinate claws.

Only the usual three setae were found on GA rather than four as noted by Viets. The Florida specimens agreed with Viets' specimens in the following specific characters: the minute patch of pores on the posterior end of AD, the arrangement of the pores on OC, the short row of pores on the sides of PD, the rough structure of the striae between AD and PD, the one slender and two spiniform setae ventrally on I-5, the absence of membranes beside the claw fossa and the presence of four setae dorsally on both III-6 and IV-6. Two females (the only adults taken) measured 374μ long (Viets, 380–412μ).

As was shown by Viets, the palpi are short, and P-3 plus P-4 are shorter than P-2. In Fig. 236 it can be seen that the rostrum extends beyond the ring of basal setae on P-4. The ventral plates are coarsely porose; and the pores form roughly pentagonal or hexagonal areas which are very prominent (Fig. 235).

Distribution. North America: Florida (Biscayne Bay, on Soldier's Key).

Curaçao.

Copidognathus (s. str.) *biscayneus*, new species

Figures 237–244

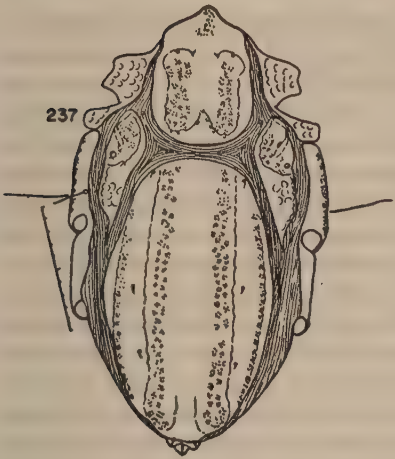
This species is represented by a single female which lacks a capitulum. It keys out to *Copidognathus manubriatus* in Viets' key (1940g: 55). That species is also inadequately described because of insufficient material. Nevertheless, the present form is not *C. manubriatus*, judging from the form of the legs and the structure of OC, and appears to occupy an isolated position.

Female. Body 346 x 204μ (L/W = 1.70). AD 106 x 77μ, nearly parallel-sided, with a rounded frontal protuberance. Three porose areas present, the anterior one containing coarse pores of irregular arrangement, the 2 posterior ones elongate and containing pores of an unusual structure (Fig. 237). The canaliculi are in groups of 6 to 12, and these open neither individually nor all through a single large pore as in the true rosette pores, but through 3, 4 or 5 irregularly arranged pores, each one of which is connected with 1, 2 or 3 canaliculi (Fig. 240, oil immersion). The three groups of canaliculi drawn are typical of the pores found in this specimen, but many of the pores are of more irregular arrangement. Often a single canaliculus opens directly to the surface. Posterior porose areas borne on a W-shaped prominence, a coarse pore and a seta at anterior end of each arm of the W. Ten to 12 deep pits at posterior end of W mark positions of internal apodemes. OC 110 x 32μ and 104 x 35μ; posterior end drawn out into a short, sharp tail extending beyond III. Corneae borne on a prominent elevation on anterior half of plate (Fig. 244). The usual 2 corneae elongate and indistinct. Posterior to these is a very distinct, solid, highly refractile body which has the appearance of, and may actually function as, a cornea. However, it appears to be homologous with the pore found in this position in most species of *Copidognathus*, and there is no such pore here or anywhere else on the plate. The usual minute pores are present, and although the majority of the canaliculi appear to open singly, some open in groups of two or three by means of a common pore, as is the rule on AD. A pair of setae between OC and AD. Posterior portion of OC faintly panelled, the panels subdivided so that the plate appears as much reticulate as panelled.

PD 222 x 133μ (not including anal papilla), oval in outline. Costae with a double row of pore panels, the pores being of the same type as those on AD and OC. The canaliculi often open individually, but two or three sometimes open by a common pore. Although the canaliculi are coarse, the pores are much smaller than those on AD and are often difficult or impossible to discern with certainty. A single row of pores just inside margins of the plate. Three pairs of setae on PD, and a fourth pair just above anal papilla. Portions of plate between and lateral to costae indistinctly panelled, but panels subdivided in such a manner that plate appears more reticulate than panelled (somewhat as in *C. acutus*, n. sp., although the two species are not closely related). Panelling more apparent at intermediate (400–600 x) than at highest magnifications (1000–1500 x), a minute canal opening into bottom of each subdivision of each panel (5 to 10 pores in each panel).

Ventral surface as shown in Fig. 241. AE and GA each with 3 pairs of setae. PE with 3 pairs of setae ventrally and 1 pair dorsally. One ventral and 1 dorsal seta are completely absent, even including the alveolus. GA 166 x 116μ; genital opening 71μ long, 66μ from anterior margin of plate. All ventral plates distinctly panelled and porose.

Figures 237–244. *Copidognathus* (s. str.) *biscayneus* new species. *237* Female: dorsum. *238* Female: IV-3, 4 and 5, ventro-lateral view. *239* Female: III-3, 4 and 5, ventro-median view. *240* Female: pores of posterior porose areas of AD. *241* Female: venter. *242* Female: leg I, median view (same scale as *243*). *243* Female: leg II, median view (slightly rotated). *244* Female: anterior portion of OC of left side.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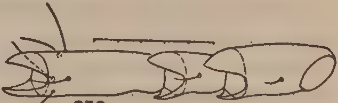
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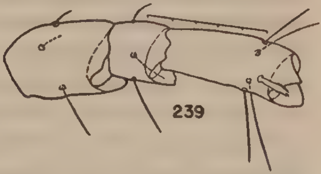
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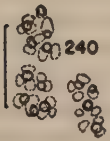
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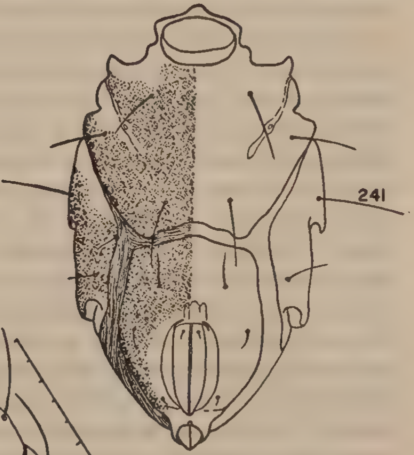
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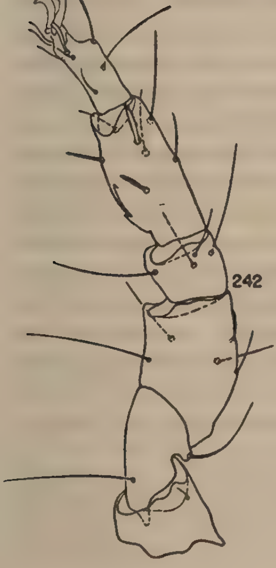
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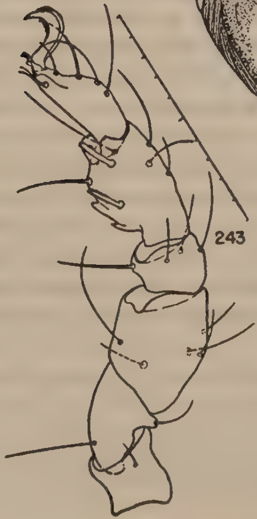
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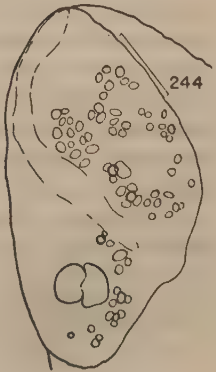
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Leg I (Fig. 242) with lamellae weakly developed on segments 3, 4 and 5. Chaetotaxy identical with that of *C.* (s. str.) *punctatissimus* (Gimbel). I-5 also with 2 sharp ventral spines as in that species, and with medial setae faintly pectinate. I-6 with bacillum and divaricate parambulacral setae but prebacillum absent; claw fossa present, the membranes greatly reduced; 3 ventral setae present. I-3, I-4 and I-5 with weakly developed lamellae. Lateral claws without a longitudinal comb, but accessory tooth containing 4 or 5 very small teeth (oil immersion). Median claw faintly bidentate and apparently worn.

Leg II (Fig. 243) also identical with that of *C. punctatissimus* in number and position of setae. I-3 and II-3 less than twice as long as high (swollen). II-5 also with 2 ventral spines, medial setae pectinate. II-6 without ventral setae, but with bacillum and divaricate parambulacral setae. II-3, II-4 and II-5 with lamellae, those on II-5 being best developed. Lateral claws with longitudinal comb and accessory "tooth" which contains 4 or 5 minute teeth as on claws of tarsus I. Median claw faintly bidentate; apparently worn. Claw fossa present, but not pronounced; membrane absent. III-1 and IV-1 greatly swollen dorsally. Segments 3, 4 and 5 of III and IV with lamellae (Figs. 238, 239). III-5 with medial member of disti-ventral pair of setae pectinate; its homologue on IV-5 smooth, slender. III-6 with 4 setae dorsally; only 3 are observed here on IV-6, but the segment is in poor position for study. A refractile spot on each tarsus suggests an alveolus from which the seta has been removed, but this cannot be ascertained. Tarsi III and IV tapering, but claw fossa and membranes absent. Medial parambulacral seta of III-6 rod-shaped, slender; lateral seta spiniform or scale-like (not in favorable position for study). One of the lateral claws on IV-6 of the left side is seen in direct ventral view, and it is identical in form with the claw of *Halacarus* (*Th.*) *basteri basteri* (Figs. 147, 148). In the present species, therefore, there is no true accessory "tooth," but only an apparent one [see the discussion under *Halacarus* (*Th.*) *basteri basteri*]. As pointed out previously, even the accessory "tooth" on I-6 is only a fragment of a comb.

Distribution. North America: Florida (Biscayne Bay, on Soldier's Key).

Copidognathus (s. str.) *angustus floridensis*, new subspecies

Figures 245–252

This keys out, with certain difficulties,[22] to *C. angustus* Viets 1936 in Viets' key (1940g: 15–27), and agrees closely with the original description of that species (Viets 1936d: 393–396). The slight differences that exist between the Florida and the Curaçao forms are greatly outweighed by the fundamental similarities, and accordingly they are considered to be related subspecifically.

Male. One of the males is 291 x 187μ (L/W = 1.56) and the other is 301μ long. Dorsal plates as in female of *C. angustus angustus* in most respects. According to Viets the panelling on AD of *C. angustus angustus* is not very distinct. That on AD of *C. angustus floridensis* is very distinct, nearly as distinct as that between the costae of PD. Although the membranous areas are greatly reduced, the closeness of the plates is exaggerated in Fig. 245, owing to the shrinkage of the delicate cuticle between the plates. Panelling of all dorsal plates very distinct (Fig. 248). All the coarse pores shown in the dorsal plates are rosette pores. Canaliculi of rosette pores minute and often irregular in arrangement, occasionally opening directly onto surface. Costae not reaching to anterior margin of PD, but reaching to a point slightly beyond anterior pair of setae; setae difficult to find because of roughness of plates. Venter as in female, except for characters of GA. Pores of anterior half of GA arranged in more definite polygonal areas than in female, but still not as definite as those on AE. Genital sclerites with 4 pairs of setae. Ten or 11 pairs of setae on each side of plate, the most anterior ones lying at a point halfway between anterior margin of opening and anterior margin of plate. Several rosette-pores lie along the postero-lateral margins of the plate, each opening into a panel-like depression in the cuticle.

Capitulum as in female (Fig. 246). Legs as in *C. angustus angustus* and *C. lamellosus.* All legs with lamellae on segments 3, 4 and 5, those on III and IV being smaller and simpler than those on I and II. Lateral lamellae of segments 3 and 4 of legs I and II larger than those

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[22] Viets stated in his key (1940g: 20): "26 (25) Rostrum nicht bis Ende des P. III reichend . . . " This leads eventually to "36 (37) Okularia hinten gerundet. Rostrum fast doppelt so lang wie breit, bis Ende des P. III reichend . . . *angustus* Viets 1936." The latter agrees with the original description and figures; the former is incorrect.

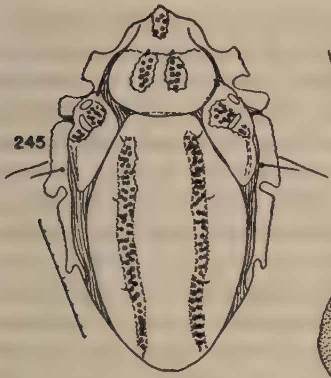
on 5. I-3 (Fig. 252) only 1.75 times as long as high (swollen); wall thick, panelled, margin finely serrate. Medial setae of I-5 pectinate. I-6 with deep claw fossa and prominent membranes, bacillum on lateral membrane, prebacillum absent, parambulacral setae divaricate. Claws faintly pectinate (oil immersion) and with accessory tooth, the median claw bidentate. II-3 also swollen (L/H = 1.42). Medial setae of II-5 serrate (oil immersion). Bacillum on lateral membrane of claw fossa. Parambulacral setae unfavorable for study, but if divaricate, one member distinctly shorter than other. Medial member of disti-ventral pair of setae of III-5 pectinate; its homologue on IV-5 slender, smooth. Lamellae on legs III and IV simple, rounded, or with slightly angular projections at the distal ends of segments 3, 4 and 5.

Remarks. *C. lamellosus* (Lohmann) 1893, *C. angustus angustus* Viets 1936 and *C. angustus floridensis*, n. subsp., form a natural group within *Copidognathus* s. str. This is evidenced, not by the mere possession of lamellae on the legs, but by the virtually identical structure of the lamellae in the three forms, and this identity is paralleled by very close similarity or identity in nearly all other structural details. Certain of the minor differences which appear to exist on the basis of the published descriptions should be re-examined to see if they are real and consistent. The three forms are separable as follows.

C. lamellosus: OC pointed posteriorly, but not tail-like. Polygonal porose areas of AE not covering entire plate but restricted to a transverse band of porose areas anterior to the epimeral pores, and a slightly wider band posterior to the epimeral pores. The anterior and posterior transverse bands may be joined by a narrow longitudinal band only as wide as two or three porose areas (sexual difference?). Genital opening of female separated from anterior margin of GA by a distance as great as length of opening. Rostrum extending to end of P-2. (Posterior cornea subdivided? Legs without pectinate setae? Claws not pectinate? These may prove to be rather tenuous characters, if not inaccurate.) Bermuda, Brazil, Australia (Sydney), Mediterranean, English Channel.

Figures 245–252. *Copidognathus* **(s. str.)** ***angustus floridensis*** **new subspecies.** ***245*** **Male: dorsum.** ***246*** **Female: capitulum, ventral view.** ***247*** **Female: venter (same scale as** ***245*****).** ***248*** **Female: portion of PD at level of second seta of right side.** ***249*** **Female: porose panels of AE.** ***250*** **Male: genito-anal plate (second pair of setae of genital sclerites omitted).** ***251*** **Male: leg II, lateral view.** ***252*** **Male: leg I, lateral view.**

Figure 253. *Copidognathus* **(s. str.)** ***septentrionalis*** **(Halbert) 1915. Female: dorsum.**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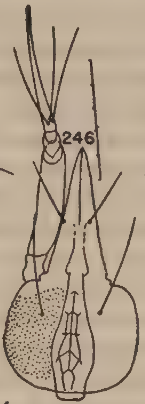
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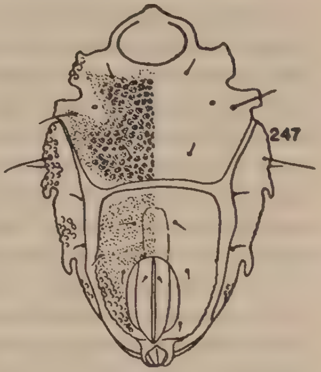
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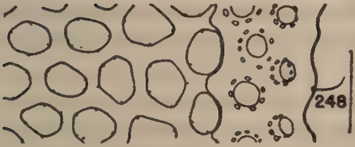
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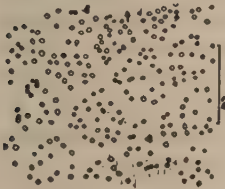
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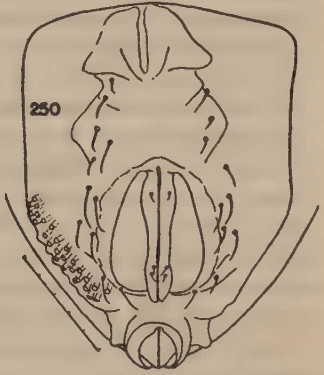
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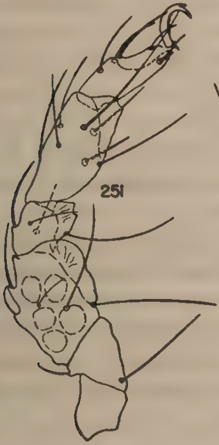
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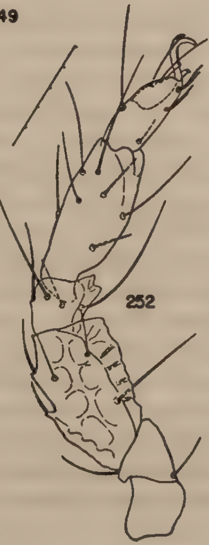
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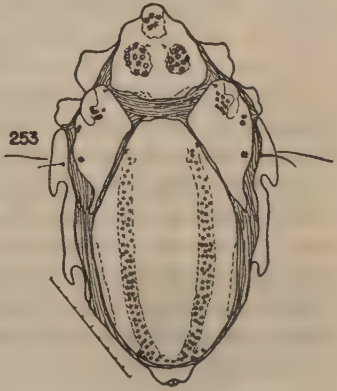
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C. angustus floridensis: OC rounded posteriorly, the posterior cornea not subdivided; claws faintly pectinate. AE uniformly covered with polygonal porose areas except at margins. Costae of PD extending slightly beyond anterior pair of setae. Genital opening of female separated from anterior margin of plate by a distance slightly less than, or equal to, length of opening. Three pairs of setae on GA. Rostrum extending to end of P-2. I-5 and II-5 with the 2 ventromedial setae pectinate. Medial member of disti-ventral pair of setae of III-5 pectinate. Florida.

C. angustus angustus: Characters agreeing with those just listed for *C. angustus floridensis* with the following exceptions. Costae of PD not extending to anterior pair of setae. Genital opening of female separated from anterior margin of plate by a distance nearly 1.5 times as great as length of opening. Rostrum reaching to end of P-3. (Viets did not figure or describe the distribution of the porose areas of AE or the setae of GA.) Curaçao.

C. simonis (Lohmann) 1907 also belongs to this group.

In the opinion of the writer, *C. lamellosus* as described by Viets (1940g) (Adriatic) differs more markedly from *C. lamellosus* as described by Lohmann (1893a) than does *C. angustus* Viets 1936. Unless more intensive work can show that reliable subspecific characters exist, it will probably be necessary to consider *C. lamellosus*, *C. angustus angustus*, *C. angustus floridensis* and *C. simonis* as different forms of a highly variable species, or at most as subspecies.

Distribution. North America: Florida (Biscayne Bay, on Soldier's Key).

Copidognathus (s. str.) *septentrionalis* (Halbert) 1915

Figure 253

Halbert 1915, 125: *Halacarus* (*Copidognathus*) *lamellosus* var. *septentrionalis*, new variety. Viets 1940g, 27, 104: *Copidognathus* s. str. *lamellosus septentrionalis* Halbert 1915.

A form living in Long Island Sound agrees well with the characters of *C. lamellosus septentrionalis* that have been pointed out in the literature. However, it differs from specimens of *C. angustus floridensis* in a number of respects. As pointed out above, the latter is very closely related to *C. lamellosus*. Accordingly, Halbert's variety is herein made a separate species, which is, nevertheless, closely related to *C. lamellosus*.

Female. The female is shown in Fig. 253. Five specimens measure 277–305μ to the tip of the frontal process. Halbert gave the length as 396–410μ. AD with 3 prominences bearing rosette pores, but in one specimen the 2 posterior areas of rosette pores are coalesced with each other. One to 3 simple pores usually found on each corner of posterior margin. OC variable in form, attenuate posteriorly and sometimes distinctly caudiform, the inner angle sometimes produced mediad, forming a sharp point; 2 groups of rosette pores present as shown. The single pore near the level of the dorsal seta of PE is often rosette-like. Costae of PD not prominent, joined posteriorly by a transverse band of rosette pores (an unusual feature indicated also in Halbert's fig. 40a). Anal papilla sometimes largely covered by PD. Rosette pores of dorsal plates usually not well developed, the canaliculi small and few in number. In one specimen there are virtually no canaliculi whatever. Ventral surface very similar to that of *C. angustus floridensis* (Fig. 247).

Rostrum shorter than in latter form, not reaching to end of P-2, the sides converging more sharply. In a female with a body length of 307μ the following measurements were obtained:

	Length	*Height*	*L/H*
I-3	65μ	34	1.91
I-5	71	28	2.54
II-3	51	31	1.65
II-5	55	23	2.83

Segments 3 and 5 somewhat less swollen than in *C. angustus floridensis*. Segments 3, 4 and 5 of all legs with pointed or rounded lamellae distiventrally, the lateral lamellae being best developed; lamellae on legs I and II no more elaborately developed than those on III and IV. III-5 and IV-5 each with medial member of disti-ventral pair of setae heavier and shorter than lateral member, but medial seta smooth, or at most very faintly pectinate, and always setiform and not scale-like. Tarsi III and IV each with 4 dorsal setae. All tarsi with claw fossa and membranes. Lateral claws I to IV with accessory tooth and very small comb (oil immersion).

Remarks. This species provides another point in favor of the elimination of *Copidognathopsis* Viets 1927. Although its closest relatives are to be found in *C. lamellosus* and related species, some specimens have remarkably attenuate ocular plates and would therefore be placed in *Copidognathopsis*. When first seen by the writer it was thought that these might be specimens of *C. oculatus*, but the form of the legs removes this possibility completely.

Distribution. North America: Rhode Island (three miles north of Block Island); New Haven County, Connecticut (Double Beach).

Ireland.

Copidognathus (s. str.) *poucheti* (Trouessart) 1893

Trouessart 1893d, 259–262: *Halacarus poucheti*, new species. Trouessart 1895a, 193–197, 199: *Halacarus poucheti*, new species. (A republication of the original description and figures.) Lohmann 1901a, 295, 298: *Halacarus* (*Copidognathus*) *poucheti* Trouessart 1894. Viets 1927a, 138: *Copidognathus* (s. str.) *poucheti* (Trouessart) 1894. Viets 1940g, 22: *Copidognathus* (s. str.) *poucheti* (Trt.) 1894.

The original description and figures of this species were published twice. It was described from material from Spitzbergen, and Trouessart stated that he had also seen specimens which were collected on *Lithothamnion* from Labrador. The present writer has not seen any mites answering the description of this species. It has not been recorded from any other region.

Copidognathus (s. str.) *gracilis* (Viets) 1936

Figures 254–256

Viets 1936d, 390–391, 409–411: *Copidognathopsis gracilis*, new species. Viets 1940g, 56: *Copidognathopsis gracilis* Viets 1936.

This species was described well by Viets (1936d: 409–411). The writer obtained a single female from Florida which keys out with little difficulty in Viets' key (1940g: 56). The following notes are added. Setae of AD minute, anterior to the single posterior rectangular group of rosette pores. Cornea or corneae scarcely discernible in dorsal view because of their anteriad orientation. OC with a seta mediad of the corneae. Costae of PD with rosette pores, PD panelled, each panel enclosing 8 to 10 pores, each in a slightly depressed area so that the

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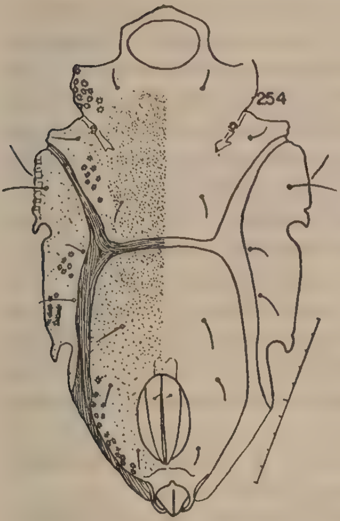
Figures 254–256. *Copidognathus* (s. str.) *gracilis* (Viets) 1936. *254* Female: venter. *255* Female: portion of PD at level of second seta. *256* Female: left epimeral pore, and surrounding rosette pores and porose panels.

Figures 257–267. *Copidognathus* (s. str.) *hummelincki* (Viets) 1936. *257* Female: PD at level of second seta, including a portion of the left costa. *258–265* Corneae of OC (*258–259* are drawn from the same mite, but all the others are from different mites. All at same magnification). *266* Male: dorsum. *267* Female: venter.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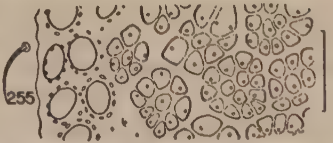
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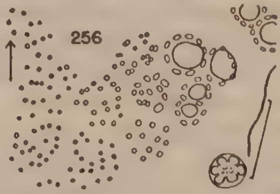
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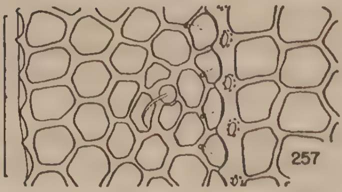
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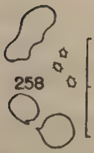
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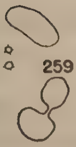
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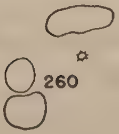
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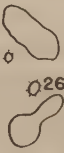
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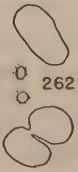
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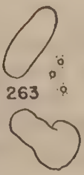
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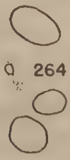
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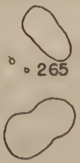
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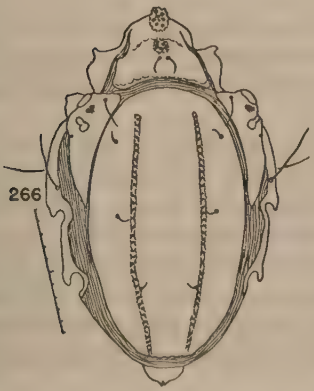
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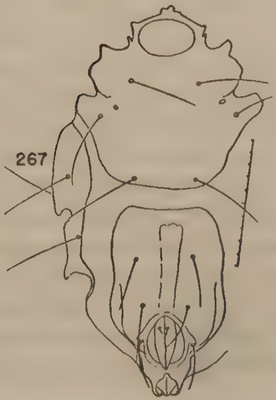
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panels appear subdivided (Fig. 255). A ventral view of the female is given in Fig. 254. The distribution of the rosette pores is unusual, especially in the presence of true rosette pores on the posterior half of AE. These are not always truly rosette-like in structure, for on the other side of the plate many of the canaliculi open directly onto the surface of AE. In fact one can find a complete series from the polygonal areas of simple, minute pores to true rosette pores. Fig. 256 shows the left epimeral pore and a small portion of AE to the left of, and anterior to, that pore. Six rosette pores can be seen anterior to the epimeral pore. The two posterior rosette pores are smaller than the others. Just to the left of these two is a group of coarse, prominent pores which under the proper circumstances of growth almost certainly would have formed a rosette pore. Such intermediate types in the transition from the ordinary type of pores to the rosette pore can be found with little difficulty.

The single female measured 298 x 159μ (L/W = 1.86). Viets gave 285 x 145μ for the dimensions of the male (L/W = 1.97).

Distribution. North America: Florida (Biscayne Bay, on Soldier's Key).

Curaçao.

Copidognathus (s. str.) *hummelincki* (Viets) 1936

Figures 257–267

Viets 1936d, 390–391, 411–415: *Copidognathopsis hummelincki*, new species. Viets 1940g, 53: *Copidognathopsis hummelincki* Viets 1936.

Viets (1936d: 411–415) gave a good account of this species, so that a full description is unnecessary here. However, the material from Florida gives an opportunity to demonstrate the variability in this species, which makes it impossible to key out certain individuals with the use of Viets' key (1940g: 52–56).

Ten females measure 284–325μ long (av. 306.1μ); five males measure 284–319μ (av. 296.4) (Viets 1936d gave the length as 278–297μ). The more significant diagnostic features are as follows. AD with only 2 small groups of rosette pores, one directly behind the other (Fig. 266). Setae of AD behind posterior group and well behind middle of plate. A pair of pores lateral to posterior group of rosette pores. OC with a seta near middle of anterior margin; usually 1 to 4 rosette pores between anterior and posterior corneae. Corneae highly variable, ranging from those in which the posterior cornea is only faintly constricted (Fig. 265) to those in which it is divided into two discrete corneae (Figs. 260, 264). The number of rosette pores medial to the corneae range from 1 to 3 in this series, and in one (Fig. 264) all the canaliculi open directly to the surface rather than into an alveolus. All dorsal plates clearly panelled, the panels sharply delimited (Fig. 257). AE and GA delicately panelled and uniformly porose, except for a very minute circular area slightly behind the margin of GA. PE with only 2 pairs of setae ventrally.

I-5 with the usual 3 ventral setae, but these are very long, slender and smooth, whereas on II-5 the 2 medial setae are faintly pectinate. III-5 with medial disti-ventral seta pectinate; its homologue on IV-5 smooth, slender. I-6 with 3 dorsal and 3 ventral setae, in addition to the bacillum and the divaricate parambulacral setae. III-6 and IV-6 each with 4 setae dorsally. Claws I to IV pectinate (oil immersion). Median claw bidentate.

Remarks. Viets (1940g: 56–58) has pointed out the similarity between *C.* (s. str.) *adriatica* and *C.* (s. str.) *tricorneata* Lohmann 1938 (Viets 1938e: 127–132). There is no doubt that *C. adriatica* is at least equally closely related to *C. hummelincki*, and probably more so. The three are separable as follows.

C. hummelincki: AD with 2 small but prominent areas of rosette pores. OC with seta near middle of anterior margin. Costae of PD reaching beyond level of first pair of setae. Panels of dorsal plates distinct, not subdivided; all dorsal setae slender. AE and GA uniformly porose. Ovipositor not reaching to anterior end of GA. PE with only 2 pairs of setae ventrally. III-6 and IV-6 with 4 setae dorsally. Florida. Also Bonaire and Aruba.

C. adriatica: AD apparently lacking rosette pores. Homologue of anterior seta of OC of *C. hummelincki* lying in the membranous area mediad from OC. Costae of PD not reaching to level of first pair of setae. Panels of dorsal plates not subdivided; all dorsal setae slender. AE with pores restricted to a V-shaped area; GA with pores restricted to a U-shaped area in the anterior half of the plate. Ovipositor not reaching to anterior margin of GA. PE with the usual three pairs of ventral setae. III-6 with 4, IV-6 with 3 setae dorsally. Adriatic Sea.

C. tricorneata: AD lacking rosette pores. Homologue of anterior seta of OC of *C. hummelincki* lying in the membranous area. Costae of PD reaching to or beyond level of anterior pair of setae. Panels of dorsal plates subdivided; setae between OC and PD, and the first and second pairs of setae of PD, short, broad and nearly scale-like. PE apparently with only 2 pairs of setae ventrally (Lohmann's sketches showed 2 on one side and 1 on the other). Ovipositor reaching beyond margin of GA. Australia (Sydney).

As shown above, the corneae are completely unreliable as a specific character in *C. hummelincki*, and it must be suspected, for the present, that the same may be true in the other two species as well.

There is no direct relationship between this species and *C.* (*Arhodeoporus*) *gracilipes* (Trouessart), despite the smooth legs (compare with Viets 1936d: 414).

Distribution. North America: Florida (Biscayne Bay, on Soldier's Key).

Bonaire; Aruba.

Copidognathus (s. str.) *caudatus*, new species

Figures 268–276

The description of this species is based on a single male and female. It keys out to *C.* (s. str.) *hummelincki* in Viets' key (1940g: 53), but there appears to be no direct relationship.

Female. Body 312 x 180μ (L/W = 1.73). AD (Fig. 268) 86 x 81μ, pyriform, slightly concave posteriorly, 2 raised groups of rosette pores present, the anterior one projecting slightly beyond the anterior margin of plate and containing only 4 or 5 poorly defined rosettes; the posterior group in the form of an inverted V and containing 20 to 25 well defined, coarse, closely-packed rosette pores. The canaliculi of these pores open not only into the sides but also into the bottom of the alveolus. The setae lie behind the posterior group of rosette pores. OC 100 x 44μ and 103 x 38μ, the attenuate posterior cornea with margins slightly less distinct than in anterior cornea. A group of rosette pores between the corneae and a seta mediad from the anterior cornea. The

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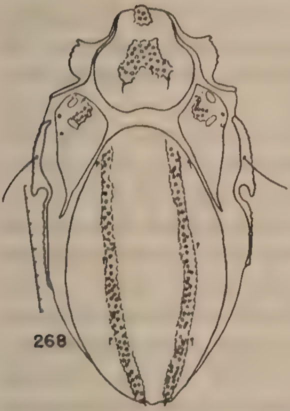
Figures 268–276. *Copidognathus* (s. str.) *caudatus* new species. *268* Female: dorsum. *269* Male: capitulum, ventral view. *270* Male: genito-anal plate. *271* Male: venter. *272* Male: porose panels of AE, just behind camerostome. *273* Female: genito-anal plate. *274* Female: portion of PD, at level of second seta. *275* Male: porose panels of AE, near posterior margin. *276* Male: porose panels of GA, halfway between anterior end of penis and anterior margin of plate.

Figures 277–279. *Copidognathus* (s. str.) *pulcher* (Lohmann) 1893. *277* Male: anterodorsal plate. *278* Male: right OC (same mite from which *277* is drawn). *279* Female: right OC (same scale as *278*).



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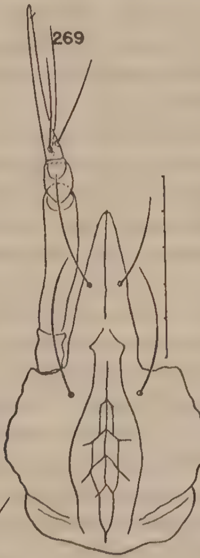

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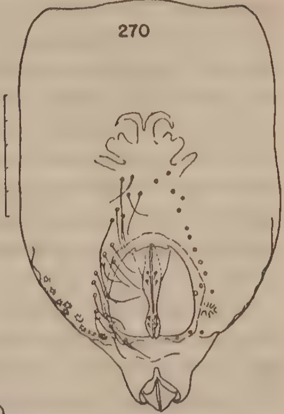

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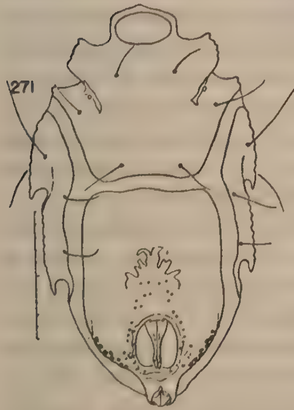

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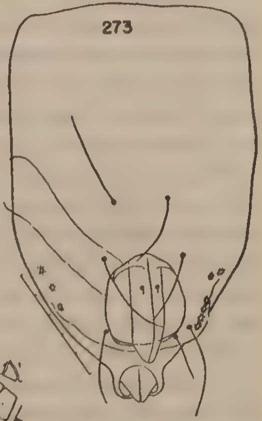

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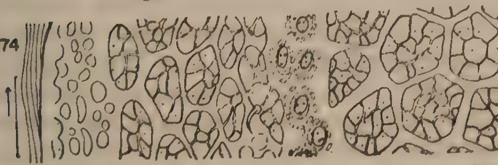

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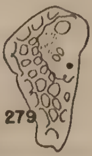

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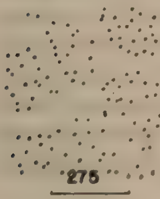

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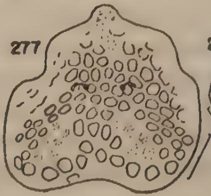

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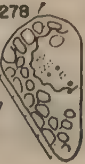

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usual pore lies laterad from the posterior cornea. PD 219 x 130μ. Costae prominent, bearing a single to double row of rosette pores. PD and OC distinctly panelled outside the elevated portions (Fig. 274), the panels less distinct than on PD.

Venter as in male, except for characters of GA. GA (Fig. 273) 167 x 106μ; distorted by an injury during the life of the mite (there is no trace of recent mechanical injury). On the right side of the plate there are the usual three setae, but on the abnormal left side the posterior seta is duplicated. The ovipositor is displaced far to the right.

Capitulum as in male. Legs not in favorable position for study, but the following features were observed. Legs relatively slender; leg I, when naturally extended, about 0.78 as long as body. I-3 and II-3 more than twice as long as high. I-5 and II-5 with medial setae pectinate (oil immersion). III-5 with medial member of ventral pair of setae pectinate; its homologue on IV-5 long, slender, but also faintly pectinate, at least in some cases. Legs without lamellae; I, II and III with shallow claw fossa, IV with neither fossa nor membranes. Claw I without longitudinal comb, but the accessory tooth appears to consist of three or four minute teeth. Claws II, III and IV with comb and accessory tooth; all median claws slender, bidentate.

Male. Capitulum (Fig. 269) 92μ long to tip of rostrum and 56μ wide. Rostrum alone 46μ long and 19μ wide near base. Sides of rostrum parallel for a short distance near base and then tapering to a sharp point. Rostrum not reaching to end of P-2, P-2 reaching to or very nearly to end of I-3 when the latter is extended. Base of capitulum panelled, densely porose, pharyngeal plate with 7 closed cells.

PE (Fig. 271) with 3 pairs of setae ventrally and 1 pair dorsally; AE and GA panelled and porose. In the postero-median portion of AE the pores are smaller, fewer in number and more widely spaced than on the rest of the plate (Figs. 272, 275). The median portion of GA from the anterior margin to the genital opening is also sparsely porose (Fig. 276), whereas the lateral portions of the plates are like the anterior and lateral portions of AE. GA (Fig. 270) 171 x 112μ. Genital opening surrounded by 35 (19 + 16) very slender setae, the most anterior of which extend to a point 0.40 the length of the plate from the anterior margin. Genital opening 43 x 35μ, removed from anterior margin of plate by a distance about 2.5 times as great as length of opening. Genital sclerites bearing 4 pairs of setae. Postero-lateral margins of GA with rosette pores. Anal papilla protruding slightly beyond PD. The single male had a body 319 x 180μ (L/W = 1.77).

Distribution. North America: Florida (Biscayne Bay, on Soldier's Key).

Copidognathus (s. str.) *pulcher* (Lohmann) 1893

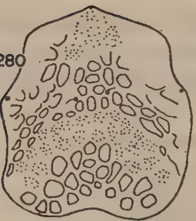
Figures 277–281

Lohmann 1893a, 22–23, 75–79: *Halacarus pulcher*, new species. Lohmann 1901a, 279, 296, 300: *Halacarus* (*Copidognathus*) *pulcher* Lohm. Viets 1927a, 139: *Copidognathus* (s. str.) *pulcher* (Lohm.). Viets 1940g, 19, 104, 106: *Copidognathus* (s. str.) *pulcher* (Lohm.).

This species was very beautifully figured in Lohmann's original description (1893a: pl. 5) and it can be keyed out easily in Viets' key (1940g: 19). The material in the writer's collection (2 females and 1 male) are not satisfactory for drawing, but some notes on variation and morphology are given here.

One of the unusual features is the absence of rosette pores. These are replaced by porose panels, the pores of which are rather coarse and open directly to the surface. On AD of one of the females, and in the male, there are two separate areas of porose panels in the position occupied by the posterior groups of rosette pores of other species (as shown in Lohmann's pl. 5, fig. 8). But in the other female these two groups are joined. The pores in the anterior group of AD of the male are rudimentary, but in the two females these are prominent (see Figs. 277, 280). These are apparently individual variations and not sexual differences. Considerable variation is seen in OC also, even in the few specimens in the writer's collection, for in the male (Fig. 278) the two posterior corneae are very rudimentary and conceivably could be absent from some individuals. In the two females all three corneae were distinct. It is clear from their size and orientation that the two posterior corneae represent the single posterior cornea of most *Copidognathus* species. In outline the posterior end of the plates ranges from rounded to angular (Figs. 278, 281). The structure of the costae of PD is precisely as shown by Lohmann, the rosette pores being replaced by porose panels which extend to within 2 or 3 panels of the anterior margin of PD. Costae 1 to 2 porose panels wide.

An unusual feature of this species is the addition of a third pair of maxillary setae at about the middle of the base of the capitulum. This seta was shown by Lohmann and is also present in the specimens seen



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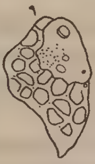

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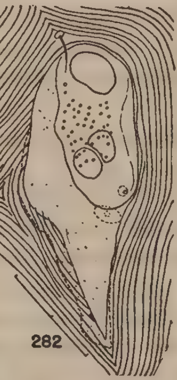

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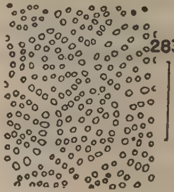

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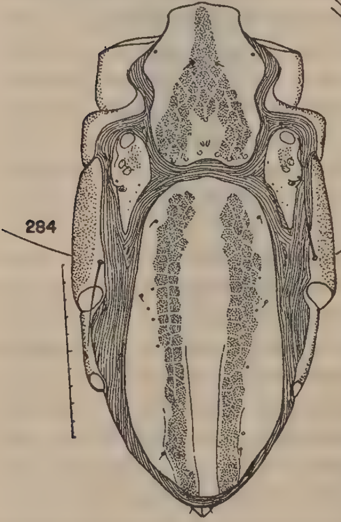

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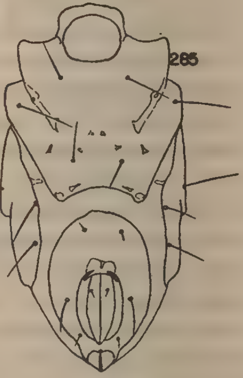

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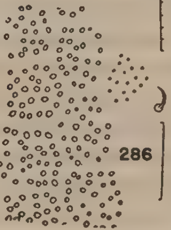

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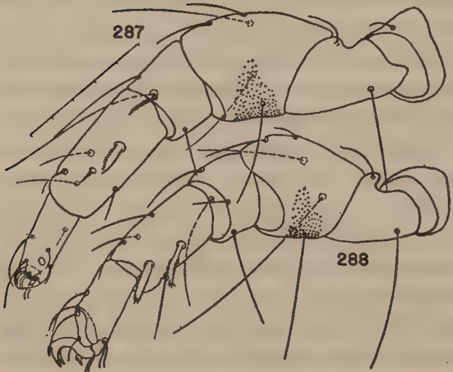

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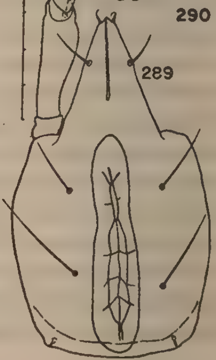

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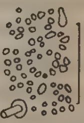

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by the writer. Lohmann did not mention pectinate setae on legs I and II, nor were they shown in his figures. Viets' (1940g: 18) statement that they are absent must be considered as entirely original, since he gave no indication of any knowledge of the species outside of Lohmann's description. Actually, both ventro-medial setae on II-5 are pectinate. On I-5 the distal member of this group appears smooth, but the proximal member is pectinate. Both III-5 and IV-5 have the medial member of the disti-ventral pair of setae scale-like and pectinate, as was noted by Lohmann.

Lengths: Male 284μ; female 312–319μ (Lohmann gave the size as 253–290μ).

Remarks: This species is closely related to *C. triops* Viets (1936d: 405–408), from Aruba, as can be seen from the similar size, form of the plates and the possession of three corneae. The distal member of the ventro-medial setae on I-5 is slender in both species, but in each the posterior member is pectinate. In both species III-5 and IV-5 have the medial member of the disti-ventral pair of setae scale-like and pectinate. The most significant differential characters are the following.

C. pulcher: Three pairs of ventral maxillary setae, the additional pair lying near middle of base of capitulum. Rostrum not reaching to end of P-2.

C. triops: With only the usual 2 pairs of maxillary setae present, one near the base of the rostrum and the other somewhat beyond the middle of the rostrum. Rostrum extending beyond P-3. Aruba, Dutch West Indies.

The characters given above to indicate the relationship between *C. pulcher* and *triops* also indicate a direct relationship between these two species and *C. magnipalpus magnipalpus* (Police) 1909 (Mediterranean, Bay of Naples) and *C. magnipalpus serratisetus* Viets 1940 (northern Adriatic). However, the relationship of these four forms to *C. magnipalpus ponticus* Viets (1936b: 199) of the Black Sea is not so clear.

Figures 280–281. *Copidognathus* (s. str.) *pulcher* (continued). *280* Female: anterodorsal plate (same scale as *277–279*). *281* Female: right OC of mite from which *280* is drawn (same scale as *277–279*).

Figures 282–290. *Copidognathus* (s. str.) *pachypus* new species. *282* Female: right OC. *283* Female: porose panels of AE. *284* Female: dorsum. *285* Female: venter. *286* Female: right costa, at level of second seta. *287* Female: leg I, ventro-median view. *288* Female: leg II, ventro-median view. *289* Female: capitulum. *290* Female: pores on base of capitulum.

More accurate figures on the type of panelling and pores would be of value here.

Distribution. North America: Florida (Biscayne Bay, on Soldier's Key).

Bermudas, Ascension, Australia (Sydney).

Copidognathus (s. str.) *pachypus* new species

Figures 282–290

This species is represented by a single female which lacks all the legs of one side. Body 294 x 150μ (L/W = 1.96), nearly twice as long as broad. AD 93 x 73μ, anterior margin nearly straight, posterior margin concave, sides constricted at level of leg II; widest portion of plate anterior to the constriction. A pair of setae and a pair of pores in widest portion of plate, several deep pits near posterior margin, marking positions of internal apodemes. OC 61 x 24μ and 58 x 23μ (L/W = 2.54 and 2.52). A seta between OC and AD. Cornea prominent, the posterior one divided to form 2 small corneae. Posterior half of OC attenuate. Under low power OC of the right side appears to have a blunt end, but under high power it can be seen that the portion of the plate not covered by striate cuticle is actually attenuate (Fig. 282), just like OC of the left side. PD 183 x 91μ (exclusive of anal papilla), with costae weakly developed except posteriorly, 3 pairs of setae present as shown. All dorsal plates lacking rosette pores but possessing porose panels. The surface of the plates outside these areas very faintly panelled, the panelling more distinct at low than at high magnifications. Each panel enclosing 5 or 6 very minute pores (shown only in Fig. 282). Panelling on OC scarcely discernible. Coarse pores lying over posterior corneae apparently incomplete, penetrating only a short way into cuticle.

AE (Fig. 285) with 3 pairs of setae, posterior margin concave. PE with 4 pairs of setae. GA 128 x 81μ; with 3 pairs of setae. Genital opening 56μ long, 46μ from anterior margin of plate. Genital sclerites projecting only slightly beyond posterior margin of opening, with a single pair of setae. AE with prominent porose panels (Fig. 283) covering plate uniformly; GA and PE also porose like AE, but panelling less distinct.

Capitulum (Figs. 289, 290) 98μ long to tip of rostrum, the base of capitulum longer than broad (63 x 56μ), densely porose (Fig. 290).

Rostrum alone 32μ long, not reaching to end of P-2 but reaching nearly to end of I-3. Three pairs of maxillary setae rather than the usual 2 pairs. Minute setae at tip of rostrum relatively long and slender. Pharyngeal plate with 7 or 8 closed panels.

Leg I (Fig. 287) very heavy, short, only 166μ long (0.57 as long as body) when in a naturally extended position. In *C. biscayneus*, n. sp., which also has relatively short legs and in which I-3 and II-3 are swollen, leg I is 0.64 as long as the body. In *C. hummelincki* leg I, when normally extended, is fully as long as the body. I-3 very short, thick, less than 1.5 times as long as high, the ventral half of segment with coarse pores as shown; lateral seta very faintly pectinate. I-4 with medial seta pectinate (oil immersion). I-5 with proximal ventromedial seta broad and coarsely pectinate; the distal one smooth. Distal end of tarsus nearly as high as base, the claw fossa nearly vertical; lateral membrane produced distally; medial membrane smaller. The lateral claws are withdrawn into the fossa so that the presence or absence of a comb and accessory tooth cannot be ascertained. Disti-dorsal setae and bacillum not in favorable position for study, 3 ventral setae present. The parambulacral setae are present laterally, but the medial ones are apparently broken off, since only an alveolus is present. Tarsus I is in an unfavorable position for study. Unfortunately, leg I of the other side is broken off, so that it is impossible to determine whether or not the rather unusual structure of the tarsus is normal.

Leg II with femur even shorter than that of leg I, less than 1.25 times as long as high. Medial seta of II-4 smooth, pectinate. Both ventro-medial setae of II-5 heavy, pectinate. II-6 with claw fossa less vertical than that of I-6 and with membranes not so well developed; 3 dorsal setae present, ventral setae absent. Bacillum and divaricate parambulacral setae present. Lateral claws with accessory tooth and with a very minute comb which does not project beyond the concave margin of the claw (oil immersion). Median claw bidentate. Femora III and IV also with a small porose area ventrally. Medial member of disti-ventral pair of setae of III-5 and IV-5 pectinate, the lateral member smooth. Tarsi III and IV with prominent claw fossa and lateral membranes. Claws as on II-6; comb discernible only with difficulty.

Remarks. As pointed out in the introduction to *Copidognathus* s. str., this species appears to be more closely related to *C.* (s. str.)

extensus Viets 1940 than to any other, although the differences between them are considerable. The two species have the following characteristic features in common. AD with lateral margins concave at level of II; posterior margin also concave. A seta lying between AD and OC. OC tricorneate and with porose area over the corneae. Rosette pores absent, replaced by simple porose panels. Rostrum not reaching to end of P-2. Basal portion of capitulum with 2 pairs of setae rather than the usual 1 pair. All legs with claw fossa and lateral membranes. Pecten scarcely discernible (or absent?); accessory tooth present. I-5 with proximal ventro-medial seta coarsely pectinate, the distal one smooth. Medial member of disti-ventral pair of setae of both III-5 and IV-5 pectinate. Body slender, about twice as long as broad. The two species are approximately equal in length. They differ as follows.

C. pachypus: Dorsal plates relatively narrower (L/W of AD = 1.25, OC = ca. 2.5, PD = 2.0). Porose areas of AD much more extensive, the costae of PD relatively broader, these being 2 to 3 panels wide; panelling very indistinct outside porose areas. Base of capitulum longer than rostrum and longer than broad. Legs heavier, shorter; femora porose ventrally.

C. extensus: Dorsal plates relatively broader (L/W of AD = 1.0, OC = ca. 1.7–1.8, PD = 1.9). AD with only 2 porose panels [probably variable as in *C. pulcher* (Lohmann), q. v.]. Costae of PD relatively narrower; apparently only 1 porose panel wide. Panelling rather distinct outside porose areas. Rostrum about as long as base of capitulum, which is broader than long. Legs more slender; femora not porose ventrally (?).

Distribution. North America: Florida (Biscayne Bay, on Soldier's Key).

Copidognathus (s. str.) *bonairensis* (Viets) 1936

Figures 291–292

Viets 1936d, 390–391, 415–418: *Copidognathopsis bonairensis*, new species. Viets 1940g, 53: *Copidognathopsis bonairensis* Viets 1936.

This species was well described by Viets, so that a redescription here is unnecessary. Figs. 291 and 292 will enable one to recognize this very unique form, the most important diagnostic features of which are as follows. AD with an elevated area in the shape of an inverted goblet, the setae lying on the anterior margin of the large posterior elevation. OC with a seta near anterior end, with a long caudiform process extending to a point between legs III and IV; 2 corneae present. PD with costae bearing porose panels (Fig. 292) of roughly rectangular form. Porose panels also lying along sides of PD, but these are less regular in form. Other porose areas of dorsal plates also made up of porose panels rather than rosette pores. Cuticle outside porose areas reticulate rather than panelled.

Ventral surface of female with all plates fused, marked with several groups of porose panels. Two pairs of maxillary setae present. I-5 and II-5 with 3 setae ventrally. All claws with comb and *apparent* accessory tooth [as in *Halacarus* (*Th.*) *basteri basteri:* p. 104]. When the claw is seen in ventral view there is no single accessory "tooth" but just a comb which curves around the outer margin of the claw.

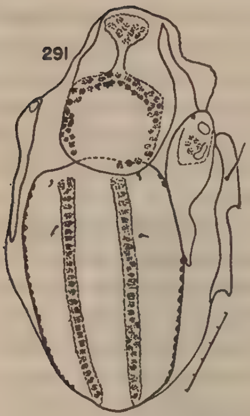
Remarks. The writer has seen only 2 specimens, both of which are females and both of which have all ventral plates fused. Viets' figs. 41 and 42 are labelled as "male," but on p. 415 he said "Das Tier, anscheinend ein Weibchen, ist dorsal 228µ lang, und 116µ breit." Viets' specimen had all the ventral plates fused. Since there is considerable question about Viets' specimen having been a male (because of his contradictory statements, and also because his drawing appears to be of a female) it is not known whether this species shows any sexual difference in the fusion of the plates. Such a sexual difference is found in *C. bairdi* (p. 145), in which the males have the ventral plates fused. The ocular plates in the specimens seen by the present writer have wider caudiform processes than those shown by Viets. Although Viets said that no comb was present, the fact that his specimen had an accessory tooth would indicate that there was at least a rudimentary comb. As is shown above, there is no discrete accessory "tooth" but only an apparent one made up of the most distal teeth of the comb.

Distribution. North America: Florida (Biscayne Bay, on Soldier's Key).

Bonaire.

Subgenus *Arhodeoporus,* new subgenus

Diagnosis. *Copidognathus* s. lat. species in which tibia I has 2 pairs of setae ventrally rather than 3 unpaired setae as in *Copidognathus* s. str. Rostrum broad at base (nearly as broad as long) with tip of rostrum scarcely extending beyond middle of P-2. Rosette pores absent (excluding the 2 epimeral pores which may be rosette-like).



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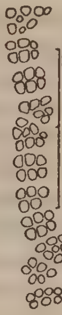

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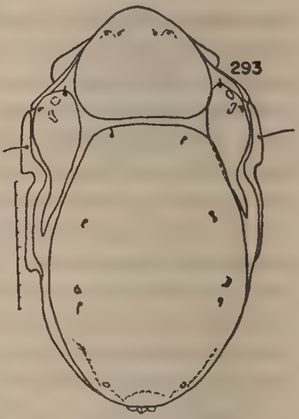

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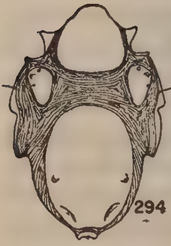

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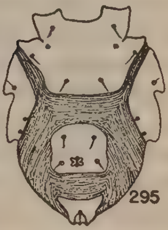

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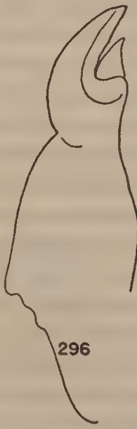

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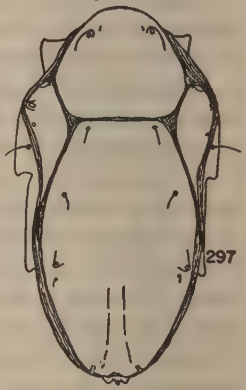

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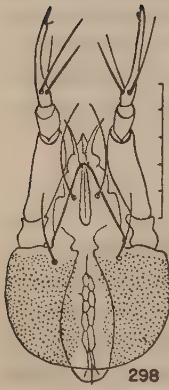

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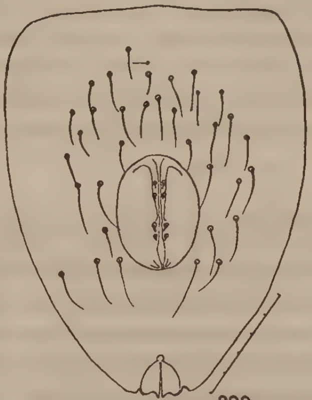

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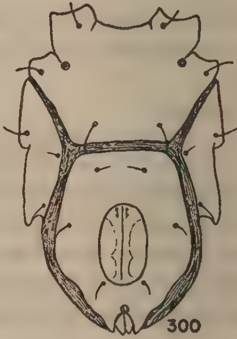


300

Ocular plate drawn out into a long, posterior, caudiform projection in the species known at present.

Type. *Copidognathus* (*Arhodeoporus*) *arenarius*, n. sp.

KEY TO NORTH AMERICAN SPECIES (ADULT)

1a. Medial margin of OC convex, projecting between AD and PD. Genital opening of male removed from tip of anal papilla by a distance greater than length of opening. Body 300–340μ long. Arenicolous, or in shallow water.
arenarius, new species; p. 175.
Massachusetts to North Carolina.

1b. Medial margin of OC nearly straight. Genital opening of male separated from tip of anal papilla by a distance less than length of opening. Body 340–415μ long. Apparently not arenicolous, and living only in deeper water.
submarinus, new species; p. 178.
Long Island Sound.

Copidognathus (*Arhodeoporus*) *arenarius*, new species

Figures 293–304

Female. Body 300–340μ long; 180μ wide. AD 110μ long, 110μ wide, bearing a pair of pores on 2 antero-lateral prominences. In some individuals (including the type) a third prominence is developed antero-medially, but this shows various degrees of reduction. Cuticle densely covered with coarse pores; panelling feebly developed or lacking and usually restricted to posterior part of plate. Posterior margin straight. OC similar in form to that of *Copidognathus gracilipes gracilipes* (Trouessart), but larger, and extending only to a point ⅔ distance between legs III and IV; caudiform process variable in width. Cornea at anterior end feebly developed, sometimes apparently lacking. A large pore at lateral angle, and posterior to this a fine pore. Cuticle irregularly porose but panelling only feebly developed. PD 200–235μ long, 150μ wide; surface porose, panelling well developed except on the 2 longitudinal ridges and around the large pores at level of leg IV. Another pair of large pores at ends of ridges. Posterior half of plate elliptical; antero-lateral margins straight, converging anteriorly; anterior margin straight or only slightly convex.

Figures 291–292. *Copidognathus* (s. str.) *bonairensis* (Viets) 1936. *291* Female: dorsum. *292* Female: porose panels of right costa, at level of second seta.

Figures 293–300. *Copidognathus* (*Arhodeoporus*) *arenarius* new species. *293* Male: dorsum (slightly rotated; specimen from Beaufort, North Carolina). *294* Deutonymph: dorsum. *295* Deutonymph: venter. *296* Female: chelicera (same scale as *304*). *297* Female: dorsum (specimen from New Haven, Connecticut). *298* Capitulum, ventral view. *299* Male: genito-anal plate. *300* Female: venter.

AE extending to or slightly beyond level of leg III, posterior margins slightly concave, lateral margins concave. Panelling well developed and similar to that on PD. PE with 3 pairs of setae ventrally and 1 pair dorsally. GA 150–160μ long, 115–125μ wide; anterior margin straight, lateral margins nearly parallel and postero-lateral margins rounded or gently sinuate; cuticle panelled; 3 pairs of setae present. Genital opening central, 66μ long and 40μ wide. Anus terminal, projecting slightly; 33μ from genital opening. Membranous areas considerably restricted, striate; plates nearly contiguous. OC-OC 100–115μ.

Capitulum 80μ long and 66μ wide; cuticle punctate but not panelled. Rostrum conical, smooth, 36μ long, reaching to a point about ¼ length of P-2 from end of that segment. Base of rostrum slightly constricted. Pharyngeal plate bearing 10 or 12 cells in a double row; lateral cells absent. Palpi (based on male) with P-2 as long as, or only slightly longer than, P-4; P-1 and P-2 sparsely and uniformly punctate; one dorsal seta on P-2, 3 on basal portion of P-4 and an extremely small seta medially near tip of P-4. Lengths of P-1 to P-4, 14, 36, 9, 32μ. Chelicerae 80μ long and 24μ high; cheliceral membrane more than ½ as long as edge of movable digit; the latter finely toothed.

Dimensions of principal leg segments as follows (given as dorsal length in μ/maximum height):

	3	*4*	*5*	*6*	*Claw*
I	75/33μ	28/23	73/25	40/12	17
II	60/25	25/20	56/18	48/12	23
III	50/17	25/15	58/15	54/12	25
IV	58/20	28/17	63/16	54/11	26

I-3 and II-3 2.3–2.4 times as long as high (not swollen); I-5 and II-5 2.0–3.1 times as long as high (above measurements from male with body length of 327μ; female essentially identical). I-3 and II-3 flattened ventrally, with 1 prominent and 1 or 2 less prominent longitudinal ridges. I-5 ventrally with a pair of slender setae distally, and another pair of setae near the middle, the medial member of which is flattened and faintly pectinate; II-5 with 2 very large, flat, pectinate setae medially and a smaller seta ventro-laterally. Both III-5 and IV-5 with a pair of setae disti-ventrally, the medial member of which is enlarged, flattened and pectinate. I-3 with 1 dorsal seta behind triangle setae, and 1 ventral seta near middle of segment. I-6 and

II-6 with very shallow claw-fossa (best developed on I-6), and each with a curved bacillum behind claw (not easily seen on leg I, but very distinct on II). Claw fossa on III and IV very faint and without membrane; bacillum lacking. Each tarsus with 2 strongly curved, nonpectinate claws, each of which has a prominent accessory tooth dorsally. All legs uniformly punctate; not panelled.

Color in life. The midgut is usually a delicate brownish-orange. As many as four pairs of elongate white spots may be seen dorsally. Under high magnification each of the dorsal white spots is seen to consist of a sac, densely packed with long filaments. The sac opens at the pore with which it is associated and the contents can be ejected by compression with a needle.

Male. The male resembles the female in most details, including size. The only discernible differences are in the form of GA, which is 165μ long and 125μ wide. Anterior edge straight, the sides nearly parallel; surface irregularly covered with coarse pores, not panelled, and with 30–35 long, slender setae. Genital opening 50μ long and 37μ wide, guarded by 8 small setae arranged in 2 groups of 4 setae. Anus terminal, projecting slightly.

Deutonymph. As in most halacarids, the nymphs vary greatly in appearance depending on the stage of development. The following description is based on a deutonymph 270μ long and 180μ wide. Dorsal plates smaller and more rounded than in adult. AD 83μ long, 81μ wide. OC rounded posteriorly, extending only to level of leg III; a single rudimentary cornea anteriorly. PD 146μ long, 108μ wide; oval in outline except at posterior end. Ventral plates also less extensive than in adult. Anal and genital plates separate. Genital plate 61μ long, 68μ wide, rounded anteriorly and square posteriorly. Anal plate 34μ long and 60μ wide. All plates faintly but distinctly panelled.

The species is compared with *C. submarinus*, n. sp., in the section on that species (p. 181).

Distribution. North America: Woods Hole, Massachusetts; New Haven County, Connecticut (Double Beach; Morris Cove [type locality]); Beaufort, North Carolina (Newport River at 3 meters, Piver's Island, Town Marsh, Harker's Island).

Copidognathus (*Arhodeoporus*) *submarinus*, new species

Figures 305–314

Female. Body 340–416μ long, 222–256μ wide, L/W = 1.53–1.66 (av. of 6 specimens 370 x 231μ, L/W = 1.61).

AD with broadest portion usually very near straight posterior margin, with a pair of pores and 1 pair of setae. OC with 1 well developed cornea and a pore, and often with a less well developed cornea behind the first. Medial margin straight or gently convex, but with no prominent medial angle. Tail of OC rather thick, extending to a point about halfway between III and IV.

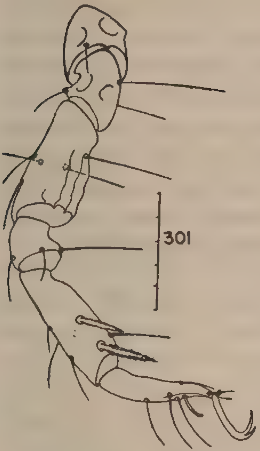
One or two very minute fragments of sclerotized cuticle often found in membranous area behind end of tail, but these never form a continuous sclerite reaching beyond IV. PD elliptical, truncate anteriorly, with 3 pairs of setae and 2 pairs of pores. Dorsal plates faintly panelled and with very minute cuticular pores except for a few areas in which the pores are very coarse. Usually 3 such areas on AD, 2 on each OC, and broad longitudinal bands on PD. The longitudinal bands on PD are not markedly elevated and owe their prominence principally to the coarseness of the pores found there. In a female with a body length of 353μ the following measurements were obtained: AD 83μ long, 125μ wide; OC 145 x 35μ, and 142 x 35μ; PD 263 x 166μ; OC–OC 130μ.

AE undivided; the posterior pair of setae at the same level as the anterior ventral pair on PE. A pair of large, simple pores between I and II. Internal apodemes prominent. GA undivided, sides parallel. Genital opening large, displaced posteriorly; anterior margin of opening often less than length of opening from anterior margin of GA. Anal papilla projecting only slightly, or not at all, beyond end of PD. Three pairs of setae present, the most anterior pair at the same level as posterior setae on PE. In the above female (353μ) GA is 169 x 123μ, the genital opening 81 x 43μ and the anterior end of the opening 68μ from the anterior margin of GA. Ventral plates faintly and uniformly panelled, without coarse cuticular pores.

Capitulum (Fig. 313) identical in form with that of *C. arenarius*, n.

Figures 301–304. *Copidognathus* (*Arhodeoporus*) *arenarius* (continued). *301* Male: leg II, median view. *302* Male: epimeral pore of left side, and surrounding porose panels. *303* Male: third dorsal gland and pore of right side, under PD. *304* Female: palp, median view.

Figures 305–307. *Copidognathus* (*Arhodeoporus*) *submarinus* new species. *305* Female: palp. *306* Female: venter. *307* Female: dorsum.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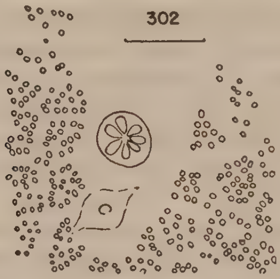
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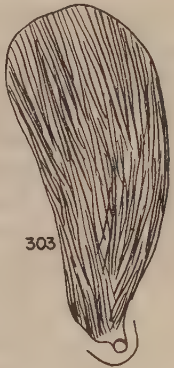
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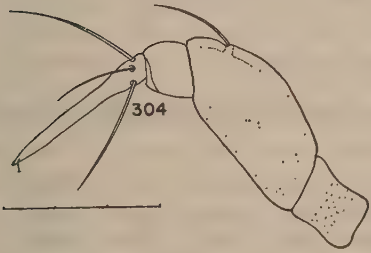
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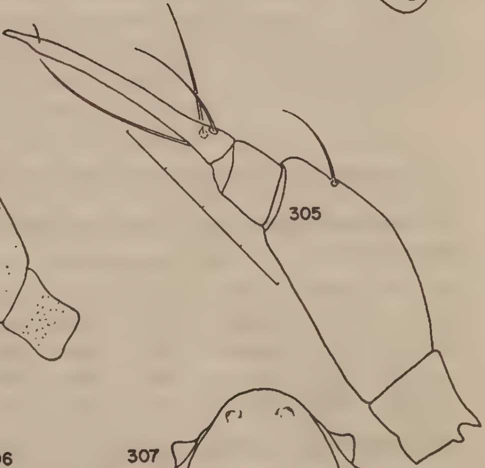
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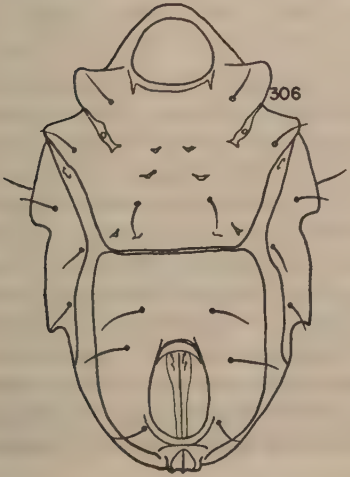
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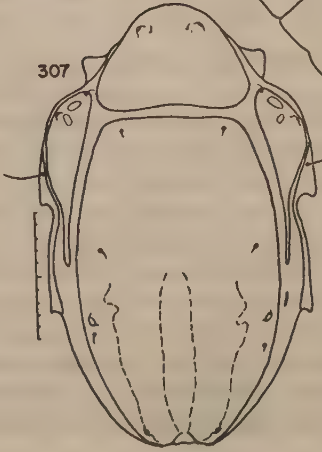
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sp. In a female with a body length of 367μ, these measurements were obtained: capitulum 90μ long to tip of rostrum and 73μ wide; rostrum alone 37μ long and 32μ wide at base, not constricted, reaching slightly beyond middle of P-2. Pharyngeal plate with 10 to 12 closed cells; lateral cells absent. Base of capitulum punctate and faintly panelled; rostrum smooth. P-1 to P-4 16, 46, 11, 49μ long respectively (body length 395μ). Chaetography of all legs identical with that of *C. arenarius*, n. sp., but setae somewhat heavier and the bacilliform setae on I and II more nearly alike than in *arenarius*.

	I				*II*				*III*				*IV*			
	d.	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*	*d.*	*v.*	*l.*	*m.*
1.	–	–	–	1	–	–	–	1	–	–	1	–	–	1	–	–
2.	1	1	–	–	1	1	1	–	1	1	–	–	1	1	–	–
3.	3	1	1	–	3	1	1	–	2	1	–	–	2	1	–	–
4.	2	2	–	–	1	1	1	1	1	1	1	–	1*	1	1	–
5.	4	4	–	–	3	1	1	2	2	2	1	–	2	2	1	–
6.	3	3	–	–	3	1	–	–	3	–	–	–	3	–	–	–

* One female has two dorsal setae on IV-4 of one side.

In a female with a body length of 395μ the following measurements were obtained:

	1+2	*3*	*4*	*5*	*6*	*Ambul.*	*Total*	*T/BL*
I	42μ	83/38	32	83	56	22	318	0.80
II	38	65/28	27	61	55	27	273	0.69
III	50	51	32	60	61	28	282	0.72
IV	53	59	35	61	65	30	303	0.77

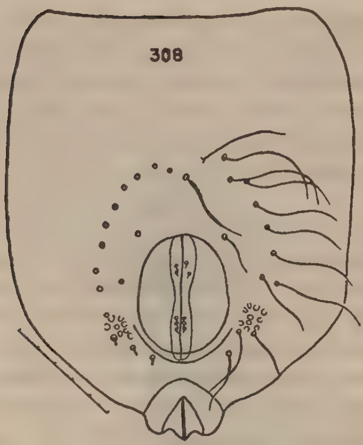
I-3 2.18 times as long as high (not swollen). Medial member of proximal pair of ventral setae on I-5 faintly pectinate. The proximal ventral seta on I-6 is often difficult to find as it is very closely applied to the ventral surface of the segment. I-6 with 3 setae dorsally and 3 ventrally in addition to bacillum and parambulacral setae. Bacillum long, only slightly curved, relatively erect, and inserted on the lateral side. Parambulacral setae not joined at base, although arising from a common area. Lateral claws not pectinate, but with a very long accessory tooth; median claw bidentate. Claw fossa represented by only a very shallow depression; membranes absent. Leg II as in *C. arenarius*, n. sp., but femur more smooth ventrally. II-5 with 2 pectinate setae medially. II-6 (Fig. 310) with bacillum on lateral side, but without prebacillum; parambulacral setae replaced by a single blunt seta on each side. Claws not pectinate, the median claw bidentate. III-5 and IV-5 with a pair of disti-ventral setae, the medial member of which is flattened and pectinate, the other slender, very long and smooth. III-6 and IV-6 with 3 setae dorsally, and with a seta and a very heavy spine at base of the ambulacrum which are homologous with the parambulacral setae on I and II. Claws III and IV as on I and II.

Male. Comparable to female in size and form. Three males measure 360–374µ long and 218–225µ wide (L/W = 1.65–1.66). The only differences in the plates lie in GA. GA parallel-sided as in female, the genital opening relatively near anus but not so close to anus as in female. Opening surrounded by 13 to 16 very slender setae on each side, and with a cluster of 8 to 10 coarse puncta on each side. In a male with a body length of 360µ GA is 174 x 141µ; the genital opening is 50 x 38µ and 93µ from the anterior margin of GA (*i. e.*, nearly twice the length of the genital opening).

Remarks. This species is highly variable in form. A number of specimens were found in which the entire body is much narrower than in the specimens on which the above description is based. But the characters of these intergrade with the characters of the common form to such an extent, even with the relatively few adults available for study, that these forms cannot be considered as constituting a distinct variety. The narrowest specimen, a female, measures 374 x 208µ (L/W = 1.80). Considerable variation is also found in the cornea (as in *C. arenarius*, n. sp.). As a rule there is a single well developed cornea, behind which sometimes lies an irregular patch of polished, refractile cuticle. The latter is often absent, however, and occasionally even the anterior cornea is not very distinct.

C. (*A.*) *submarinus*, n. sp., *arenarius*, n. sp., and *gracilipes gracilipes* (Trouessart) are quite similar in most respects. Using Viets' descriptions and figures (1927a: 145–148; 1940g: 59–60) as a basis of comparison, the three species can be differentiated as follows.

C. submarinus: Medial margin of OC not projecting between AD and OC, but relatively straight. Second dorsal seta lying in anterior angle of OC, the third dorsal setae in PD. OC not extending to level of insertion of leg IV. Costae of PD usually not projecting prominently. Posterior setae of AE about 4 times as far from hind margin of plate as the most posterior apodemes. Porose panels uniformly developed over entire surface of plate. PE with 4 pairs of setae.



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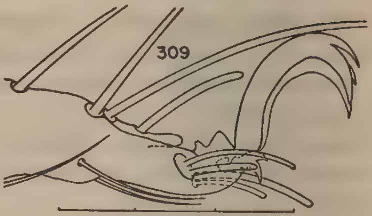

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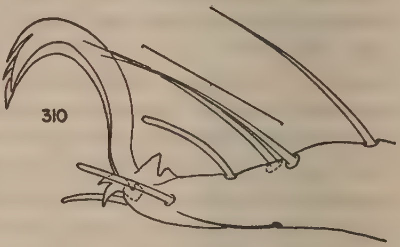

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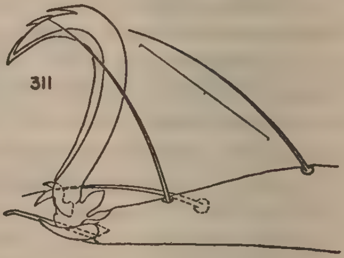

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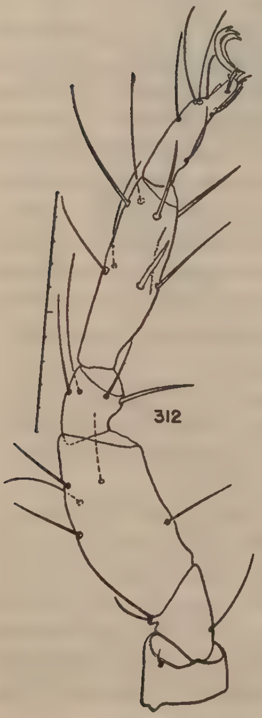

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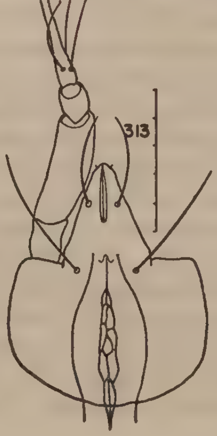

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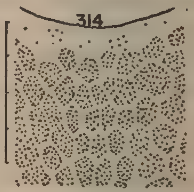

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Genital opening of female removed from anterior margin of GA a distance nearly as great as length of opening. Genital opening of male separated from end of anal papilla by a distance less than length of opening.

C. arenarius: As above, except for the following features. Medial margin of OC distinctly convex, projecting between AD and PD. Genital opening of male removed from tip of anal papilla by a distance greater than length of the opening.

C. gracilipes gracilipes: Medial margin of OC projecting between AD and PD, distinctly convex. Second and third dorsal setae lying in the membranous area. OC extending beyond insertion of IV. Costae of PD projecting prominently. Posterior setae of AE near edge of plate, at same level as the most posterior apodemes. Coxal areas I and II of each side with an area of prominent porose panels. PE with 5 pairs of setae. Genital opening of female removed from anterior margin of GA by a distance much greater than (1.5 times) the length of the opening.

Distribution. North America: Rhode Island (3 miles north of Block Island, at 34 meters).

Genus *Agaue* Lohmann 1889

Lohmann 1889a, 270, 294, 318, 338, 353–355: *Agaue*, new genus. Lohmann 1893a, 67–75, 79, 81–82: "*Chevreuxi*-Gruppe." Trouessart 1894a, 174: "Groupe *Chevreuxi*" Lohmann 1893. Lohmann 1901a, 286–287, 335: *Polymela*, nom. nov. Viets 1927a, 85, 87, 90–94, 169: *Agaue* Lohmann 1889. Viets 1928c, 57–60, 72: *Agaue* Lohmann 1889. Viets 1940g, 62–75, 111, 119, 121–122, 128: *Agaue* Lohmann 1889.

Diagnosis. Body and legs often with elaborate lamellae. Capitulum often reaching to or very nearly to end of I-3. Palpi relatively straight (see key to genera), distinctly 4-segmented, attached to capitulum laterally, so that bases of palpi are clearly visible in ventral view and are separated from each other by a distance greater than width of P-1. Combined length of P-3 and P-4 less than length of P-2, but greater than one-third length of P-2. P-3 never with a thick medial seta. Rostrum usually distinctly parallel-sided, or even slightly

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Figures 308–314. *Copidognathus* (*Arhodeoporus*) *submarinus* (continued). *308* Male: genito-anal plate. *309* Female: I-6, median view. *310* Female: II-6, median view. *311* Female: III-6, lateral view (same scale as *309–310*). *312* Female: leg I, median view. *313* Female: capitulum, ventral view. *314* Female: porose panels of AE, just behind camerostome.

broader near distal end than near middle. Leg I without heavy, rod-shaped setae medially and ventrally. Middle piece of ambulacrum articulating directly with end of tarsus; carpite absent.

Type. *Agaue parva* (Chilton) 1883; by monotypy.

Remarks. A single species is known from North America.

Agaue nationalis (Lohmann) 1893

Figure 315

Lohmann 1893a, 14, 22–23, 68, 70–73: *Halacarus nationalis*, new species. Trouessart 1900b, 46: *Leptospathis nationalis* (Lohmann). Lohmann 1901a, 275, 277, 287–288: *Halacarus* (*Polymela*) *nationalis*. Viets 1928c, 58–59: *Halacarus nationalis* Lohm. Viets 1940g, 63, 68–69: *Agaue nationalis* (Lohm.) 1893.

This is one of the most beautiful of all mites, owing to the elaborate development of lamellae on the body and legs (Fig. 315). These develop as extensions of the walls of panels, so that the cavity of the panel, instead of being a shallow depression, is a long, tubular chamber, tapering gradually toward the edge of the lamella, where it often opens through a small circular pore. The species can be differentiated from other species of the genus by the greatly swollen ends of the tibiae of all the legs, the complete absence of setae from P-3, and the very elaborate development of the lamellae. The rostrum reaches to or slightly beyond the middle of P-4, and the tips of the palpi extend beyond the end of I-3.

Distribution. North America: Florida (Biscayne Bay, on Soldier's Key). Bermudas.

Northeastern Brazil.

Genus *Agauopsis* Viets 1927

Viets 1927a, 85, 87, 90, 94, 169: *Agauopsis*, new genus. Viets 1927b, 5, 56: *Agauopsis* Viets. André 1938b, 168–169: *Agauopsis* Viets.

Diagnosis. Middle piece of claw articulating directly with tip of tarsus, carpite absent. Palpi distinctly 4-segmented; P-3 plus P-4 shorter than P-2 in probably all species. Palpi attached laterally,

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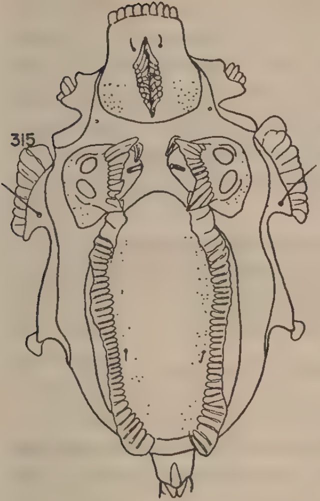
Figure 315. *Agaue nationalis* (Lohmann) 1893. Male: dorsum (same scale as *318*).

Figure 316. *Agauopsis brevipalpus brevipalpus* (Trouessart) 1889. Female: dorsum (slightly rotated).

Figures 317–321. *Agauopsis borealis* new species. *317* P-2, 3 and 4, dorsal view, right palp. *318* Female: dorsum. *319* Female: capitulum, lateral view. *320* Female: palp, median view (palp probably slightly flexed). *321* Female: venter.



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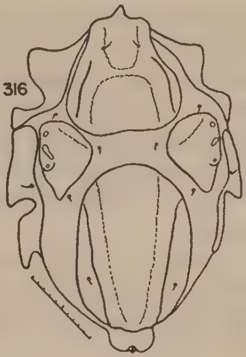

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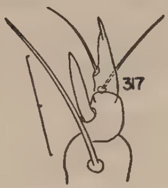

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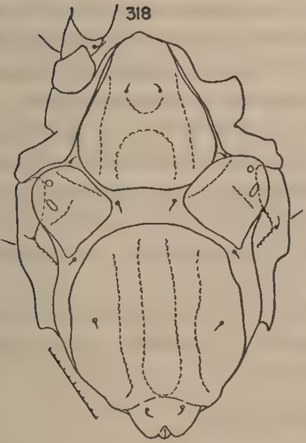

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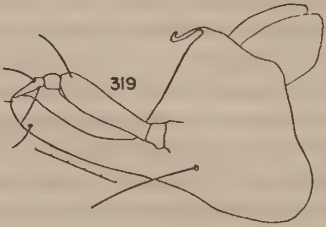

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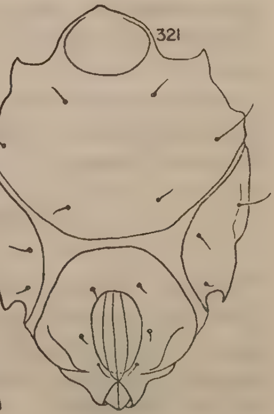

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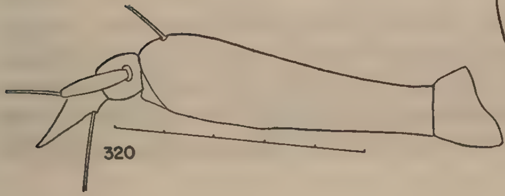

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separated at their bases by a distance greater than width of P-1, relatively straight (see key to genera, p. 21); P-3 often with a heavy medial seta. Rostrum usually tapering very slightly, rarely completely parallel-sided and never broader distally than near middle. Capitulum relatively short, never reaching to end of I-3. Leg I often with heavy, spike-shaped setae on medial and ventral surfaces.

Type. *Agauopsis brevipalpus* (Trouessart) 1889 (by original designation).

Remarks: Only two forms, *A. brevipalpus brevipalpus* and *A. borealis*, n. sp., are known from North America. These are compared in the description of *A. borealis,* in lieu of a formal key.

Agauopsis brevipalpus brevipalpus (Trouessart) 1889

Figure 316

Trouessart 1889b, 181: *Agaue brevipalpus.* Viets 1928c, 60–64: *Agauopsis brevipalpus brevipalpus* (Trt.); and *A. brevirostris* s. str. (lapsus calami).

Agauopsis brevipalpus brevipalpus and *A. b. pontica* (Chichkoff) 1907 have been treated so extensively by previous workers (most critically by Viets, 1928c: 60–64; 1940g: 74, 76, 78–81, *etc.*; also by Lohmann 1893a: 22, 23, 85, 87) that no further treatment is necessary here.

One of the Florida specimens is drawn in dorsal view (Fig. 316) to aid in distinguishing it from *A. borealis*, n. sp., with which it is compared below. Three females measure 409–422µ long (to the tip of AD), whereas six males measure 325–367µ.

Distribution. North America: Florida (Biscayne Bay, on Soldier's Key).

Brazil (northeastern), Bermudas, Azores, Canary Islands, French Atlantic, Ireland, Mediterranean, northern Adriatic, Black Sea, Australia (Sydney).

Agauopsis borealis, new species

Figures 317–326

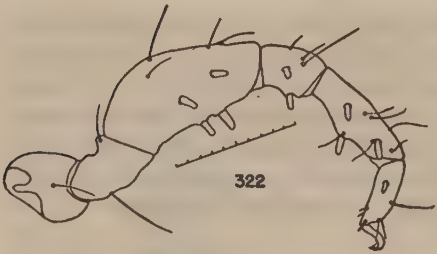
Female. The only intact females in the author's collection measure 471 x 322 (L/W = 1.46) and 500 x 346µ (L/W = 1.44), the length measured to the minutely rounded tip of AD. In the shorter specimen the following measurements were obtained: AD 183 x 158, OC 108 x 88 and 110 x 96, PD 215 x 215µ, the latter not including the anal papilla.

AD depressed around margins in such a way as to form an H-shaped elevated area. Depressed areas panelled and porose. OC with portion on which the 2 corneae are found are porose only; rest of plate both porose and panelled. PD with costae nearly or completely parallel, not diverging anteriorly. Costae porose and only moderately prominent; rest of plate panelled and porose. In the specimen drawn in Fig. 318, the membranous area is considerably contracted. The plates do not overlap.

AE (to posterior margin of camerostome) as long as GA. PE with 3 pairs of setae ventrally and 1 pair dorsally. GA with 3 pairs of setae, the posterior pair very slender. Internal suckers as shown in Fig. 324. Ventral plates uniformly porose (Fig. 325), very faintly panelled.

Capitulum 171μ long to tip of rostrum (body length 500μ) and about 89μ wide. Rostrum alone 88μ long and 26μ wide near base, reaching very nearly to tip of palp. In Fig. 319 the palp is slightly flexed. The specimen was dissected in glycerine without treatment of any kind. Two specimens treated with trypsin show that the palpi extend about 5 or 6μ beyond the rostrum. This is, therefore, a very tenuous diagnostic character. Posterior pair of rostral setae 2 or 3 times the dorsal length of P-1 behind insertion of palp. P-1 to P-4 7, 68, 9, 19μ long; P-2 16μ high (body length of specimen unknown). Medial seta of P-3 very heavy, much longer than P-3 itself, and about ⅓ as high. P-4 with only 2 basal setae.

Chaetography of leg I (Fig. 322) identical with that of *A. brevipalpus brevipalpus* as figured by Viets (1940g: 79). I-3 not swollen (L/H = 2.2). I-6 (Fig. 323) with bacillum but without a prebacillum, unless the large process anterior to the bacillum represents a greatly modified prebacillum [as in *Halacarus* (*Th.*) *subterraneus;* Fig. 175]. Parambulacral setae divaricate. Lateral claws not pectinate, accessory tooth present. Median claw bidentate. Chaetography of leg II also identical with that of *H. brevipalpus brevipalpus* (see Viets 1940g: 79). Heavy ventral setae of II-5 faintly pectinate. II-6 without medial or ventral setae. Lateral parambulacral seta divaricate, with ventral member less than half as long as dorsal member (Fig. 326). Although no bacillum can be seen on II-6, there is such a well developed cuticular canal anterior to the medial disti-dorsal seta that it seems most likely that a bacillum had been present but was broken off. A sharply-bent, minute bacillum is found in this position in *A. brevipalpus*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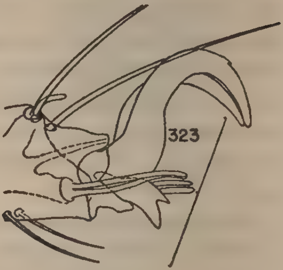
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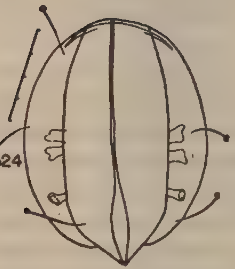
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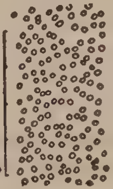
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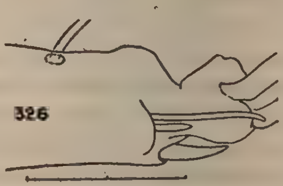
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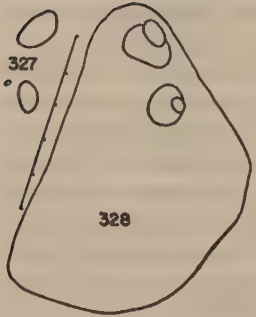
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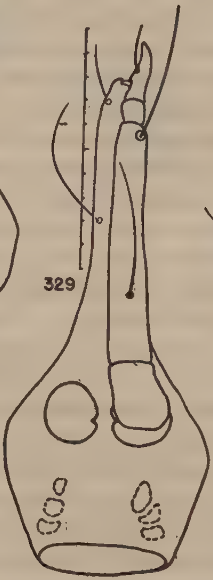
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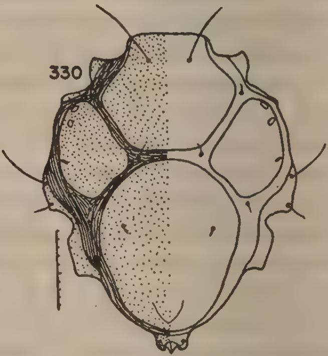
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brevipalpus. Lateral claws pectinate and with accessory tooth, median claw absent. III-5 and IV-5 with a pair of heavy, faintly pectinate setae disti-ventrally. III-6 and IV-6 with only the lateral parambulacral setae present, spiniform. Claws III and IV pectinate, median claw absent. Claw fossa on I-6 very small, other tarsi only tapering.

Remarks. This species appears to resemble *A. brevipalpus brevipalpus* (Trouessart) more closely than any other, although it differs in several respects. The most apparent diagnostic features are as follows.

A. borealis: AD with H-shaped area distinct but not sharply elevated above the plate, well removed from sides of plate. PD with costae parallel. Palpi slightly longer than rostrum. Spiniform setae of leg I relatively small.

A. brevipalpus brevipalpus: AD with posterior arms of H-shaped area very prominent, their outer edges sharply elevated above the surface of the plate and forming a virtual keel. PD with costae distinctly divergent anteriorly. Palpi slightly shorter than rostrum. Spiniform setae of leg I relatively large.

Viets (1928c: 60–65) gave a detailed comparison of *A. brevipalpus brevipalpus* with *A. brevipalpus pontica.* *A. borealis* is more closely allied to the former.

Distribution. North America: New Haven County, Connecticut (Morris Cove, type locality); Solomon's Island, Maryland; Beaufort, North Carolina (Newport River at 2.5 meters; Town Marsh; Harker's Island).

SUBFAMILY LOHMANNELLINAE VIETS 1927

Diagnosis. Middle piece of claw articulating directly with end of tarsus; carpite absent. Palpi attached to capitulum dorsally, separated by an interval not greater than width of base of P-1, distinctly 4-segmented. Rostrum about as long as palpi in uncompressed specimens, relatively uniform in width, opposed to downwardly turned elongate palpi. Rostrum at least three times as long as high. Marine or fresh water. Predaceous. Probably cosmopolitan.

Figures 322–326. *Agauopsis borealis* (continued). *322* Female: leg I, median view. *323* Female: I-6, lateral view. *324* Female: genital opening. *325* Female: portion of cuticle from center of AE. *326* Female: II-6, ventro-lateral view.

Figures 327–330. *Lohmannella falcata* (Hodge) 1863. *327* Male: corneae (same scale as *328*). *328* Deutonymph: ocular plate. *329* Male: capitulum, dorsal view. *330* Male: dorsum.

Genus *Lohmannella* Trouessart 1901

Hodge 1863, 298–299, 302–303: *Leptognathus*, new genus (preoccupied). Lohmann 1901a, 276, 280, 303, 336: *Trouessartella*, new name (preoccupied). Trouessart 1901a, 250, 263–264: *Lohmannella*, new name. Viets 1940g, 91–94, 111, 115, 121, 130: *Lohmannella* Trouessart 1901.

Diagnosis. Capitulum sometimes very long, about $^1/_6$ to $^1/_3$ as wide as body. Rostrum about as long as palpi and uniform in width beyond middle; rounded terminally, not broadened, opposed to downwardly turned palpi. Palpi distinctly 4-segmented, attached to base of capitulum dorsally, separated basally by an interval no greater than width of P-1. Genital suckers external.

Type. *Lohmannella falcata* (Hodge); by monotypy.

Lohmannella falcata (Hodge) 1863

Figures 327–330

Hodge 1863, 298, 302–303: *Leptognathus falcatus*, new species. Brady 1875, 307: *Raphignathus falcatus* (Hodge). Murray 1876, xiii, 208–209: *Halacarus falcatus* (Hodge). Trouessart 1888a, 754: *Leptognathus falcatus*. Lohmann 1889a, 275, 316, 355, 357–360, 363, 371, 383: *Leptognathus falcatus* Hodge; 286–290, 292, 294, 296–297, 355–357, etc.: *Leptognathus marinus*, new species. Trouessart 1896c, 328, 330, 348, 350–352: *Leptognathus falcatus* Hodge. Lohmann 1901a, 277, 279, 302–304, 351: *Trouessartella falcata* (Hodge) 1863. Trouessart 1901a, 250, 264: *Lohmannella falcata*. Lohmann 1907a, 364–365, 371, 391–392, 396–398, 402–403, 405, 407–409: *Lohmannella falcata* Hodge. Halbert 1915, 127: *Trouessartiella falcata* (Hodge). Viets 1927a, 96, 148, 152–153, 155–156, 159–161, 164, 166, 168–171: *Lohmannella falcata* (Hodge) 1863. Viets 1927b, 6, 28–29, 47, 54–55, 66: *Lohmannella falcata*. Schulz 1933, 102–104: *Lohmannella falcata*. Viets 1940g, 91–92, 98–101, 103, 105, 107, 120–121: *Lohmannella falcata* (Hodge) 1863.

The male shown in Fig. 330 has a body 374 x 291μ (L/W = 1.28); length to tips of palpi 585μ. AD pentagonal, bearing a pair of long, slender setae. OC broadly rounded laterally, with 2 reduced corneae anteriorly and a slit-like pore just behind middle of lateral margin. Corneae distinctly smaller than those of deutonymph and sometimes almost lacking. PD ovate, distinctly broader anteriorly than posteriorly, widest portion ⅓ length of plate from anterior end. A single pair of setae at level of widest portion of plate. Anal papilla completely terminal, with a pair of minute setae dorsally. Dorsal plate faintly punctate, not panelled. Membranous area restricted, striate, with 3 pairs of setae near corners of OC. AD 138μ long, 153μ wide; OC 120 x 90μ, and 113 x 86μ; PD 199 x 164μ; AD-PD ca. 17μ; OC-OC 90μ. Capitulum as shown in Fig. 329.

The deutonymph has a different type of cornea from that found in the adult. The corneae are larger and more complex, consisting of 2 large circular or oval areas, each partly enclosing a smaller, very highly refractile portion. The difference can be seen by comparing Fig. 327 with 328, which are drawn at the same magnification.

Distribution. North America: St. Andrews, New Brunswick; Rhode Island (3 miles north of Block Island, at 34 meters).

Baltic, North Sea, Shetland Islands, Ireland, French Atlantic, Mediterranean, Adriatic, Black Sea, Kerguelen, Antarctic.

ECOLOGY

INTERRELATIONSHIPS OF THE FAUNAE OF THE EASTERN COAST OF NORTH AMERICA

The most intensively studied areas on the eastern coast of North America are: New Brunswick (St. Andrews), Long Island Sound (Connecticut and Rhode Island), Chesapeake Bay (Solomon's Island, Maryland), North Carolina (Beaufort) and southern Florida (Biscayne Bay). Miscellaneous records from Massachusetts (Woods Hole), and Maine (Casco Bay and Eastport) are also included, as are the records of previous workers.

A total of 41 species, subspecies and varieties of Halacaridae are now recorded from eastern North America and Greenland, as compared with the four which were known previously (Table I). Of the latter, two [*Halacarus* (*Thalassarachna*) *basteri basteri* and *Copidognathus* (s. str.) *punctatissimus*] were rediscovered in the course of the present work, whereas the other two [*Rhombognathus notops* and *Copidognathus* (s. str.) *poucheti*] were not. Of the 41 forms, 27 were known from previous works and 14 are newly described. The number of North American genera and subgenera has been increased from three to eleven. Of these, three are newly described herein, but each of these contains representatives which were previously known from Europe.

TABLE I. DISTRIBUTION OF THE MARINE HALACARIDAE OF EASTERN

Genera, Subgenera, Species, Subspecies, and Varieties	*S. Florida*	*North Carolina*	*Chesapeake Bay*	*Conn.-Rhode Island*	*Massachusetts*	*Maine*	*New Brunswick*	*Labrador*	*Greenland*
Rhombognathus	+	+	+	.	.	.	.	.	+
magnirostris magnirostris	+	.	+	.	.	.	.	.	.
magnirostris lionyx	.	+	.	.	.	.	.	.	.
notops	.	.	.	.	.	.	.	.	+
Rhombognathides	.	.	.	+	+	.	+	.	.
pascens	.	.	.	+	+	.	.	.	.
seahami	.	.	.	.	+	.	.	.	.
mucronatus	.	.	.	+	.	.	+	.	.
merrimani merrimani	.	.	.	.	.	.	+	.	.
merrimani needleri	.	.	.	.	.	.	+	.	.
Metarhombognathus	.	+	.	+	.	.	+	.	.
armatus americanus	.	+	.	+	.	.	+	.	.
Isobactrus	.	.	.	+	.	.	.	.	.
setosus	.	.	.	+	.	.	.	.	.
levis	.	.	.	+	.	.	.	.	.
hutchinsoni	.	.	.	+	.	.	.	.	.
Halacarus s. str.	+	+	+	+	.	.	.	.	.
ctenopus	+	.	.	.	.	.	.	.	.
actenos	+	.	.	.	.	.	.	.	.
frontiporus	.	.	.	+	.	.	.	.	.
anomalus	.	+	+	+	.	.	.	.	.
H. (Thalassarachna)	.	.	.	+	.	+	+	.	+
basteri basteri	.	.	.	+	.	+	+	.	+
longipes	.	.	.	+	.	+	.	.	.
balticus	.	.	.	+	.	.	+	.	.
capuzinus	.	.	.	+	.	.	+	.	.
subterraneus	.	.	.	+	.	.	.	.	.

The entire number of forms from each region must be considered in the light of the effort expended in collecting. Thus, the 19 forms known from Long Island Sound were collected over a period of nearly three years, during which time scores of samples were examined, from both intertidal and subtidal habitats. On the other hand, 15 forms were taken in one small collection from Soldier's Key, Biscayne Bay, Florida, and all but one of these (*Copidognathus pulcher*) were found

North America. See Text, p. 191

Genera, Subgenera, Species, Subspecies, and Varieties	*S. Florida*	*North Carolina*	*Chesapeake Bay*	*Conn.-Rhode Island*	*Massachusetts*	*Maine*	*New Brunswick*	*Labrador*	*Greenland*
Agaue	+	.	.	.	.	.	.	.	.
nationalis	+	.	.	.	.	.	.	.	.
Copidognathus s. str.	+	+	.	+	.	.	.	+	.
punctatissimus	.	+	.	+	.	.	.	.	.
acutus	.	+	.	.	.	.	.	.	.
bairdi	+	.	.	.	.	.	.	.	.
curassaviensis	+	.	.	.	.	.	.	.	.
biscayneus	+	.	.	.	.	.	.	.	.
angustus floridensis	+	.	.	.	.	.	.	.	.
septentrionalis	.	.	.	+	.	.	.	.	.
poucheti	.	.	.	.	.	.	.	+	.
gracilis	+	.	.	.	.	.	.	.	.
hummelincki	+	.	.	.	.	.	.	.	.
caudatus	+	.	.	.	.	.	.	.	.
pulcher	+	.	.	.	.	.	.	.	.
pachypus	+	.	.	.	.	.	.	.	.
bonairensis	+	.	.	.	.	.	.	.	.
C. (*Arhodeoporus*)	.	+	.	+	+	.	.	.	.
arenarius	.	+	.	+	+	.	.	.	.
submarinus	.	.	.	+	.	.	.	.	.
Agauopsis	+	+	+	+	.	.	.	.	.
brevipalpus brevipalpus	+	.	.	.	.	.	.	.	.
borealis	.	+	+	+	.	.	.	.	.
Lohmannella	.	.	.	+	.	.	+	.	.
falcata	.	.	.	+	.	.	+	.	.
Totals:	15	7	3	19	3	2	8	1	2

on two small bunches of *Halimeda*, a calcareous green alga. Had collections been made in Florida on the same scale as those in Long Island Sound, two or three times the number of species probably would have been found. Six days of intensive collecting at Beaufort, North Carolina, during which 26 samples were taken from a wide variety of habitats, yielded only seven species. Only three species were taken at Solomon's Island, Maryland, in three days. Equivalent collecting in habitats in the vicinity of New Haven probably would have yielded 12 to 15 species. To be sure, the fauna at Solomon's Island (salinity 10–12°/₀₀) is not to be compared directly with that at the mouth of Chesapeake Bay, but it seems likely that even on the open coast the fauna would not be as rich as that to the north. Twelve samples from the intertidal zone at St. Andrews, New Brunswick, contained eight species, indicating that the fauna there is probably about as rich as that around New Haven. Therefore, the Florida fauna is certainly the richest on our eastern coast, that of the New England coast is the second richest, and intermediate regions are the poorest.

The most striking feature noticeable in Table I is the complete lack of correlation between the faunae of Florida and the New England-New Brunswick coast, there being not one species common to both regions. In fact, only three of the 11 genera are found in both regions. The following genera or subgenera of the New England-New Brunswick coast are lacking in southern Florida: *Rhombognathides*, *Metarhombognathus*, *Isobactrus*, *Halacarus* (*Thalassarachna*), *Copidognathus* (*Arhodeoporus*) and *Lohmannella*. The genera *Agaue* and *Rhombognathus* are lacking in the north.

The fauna at Beaufort is much more closely related to the northern fauna than to that of Florida, for of the seven forms taken at Beaufort, five are northern species, one is endemic and only one is subspecifically related to a Florida species. The genus *Rhombognathus* is found there, whereas it has not been found by the writer north of Chesapeake Bay. The paucity of the fauna at Beaufort is due to a dropping out of entire genera or subgenera. Thus, *Halacarus* (*Thalassarachna*), *Rhombognathides*, *Isobactrus* and *Lohmannella* are completely lacking there, whereas these four groups contribute a total of 14 forms to the fauna of the New England-New Brunswick region. At the same time, Beaufort does not have the extreme development of *Copidognathus* (s. str.) which is seen in southern Florida.

The structure of the North Carolina coast is very complicated, the main coast being separated from the open Atlantic by an almost continuous series of offshore bars. The intervening sounds communicate with the Atlantic through a few narrow inlets, numerous rivers open into the sounds, and therefore the water in these sounds is less saline than that outside the bars. McDougall (1943: 330) stated that the salinity at Piver's Island is normally about 30°/₀₀, with the extremes at 8 and 38°/₀₀. In the open ocean the salinity is usually 35 to 36°/₀₀ and with a smaller range of variation. Water temperatures are also influenced by the structural features of the coast. At Cape Lookout Lighthouse the surface water temperature ranges from 25–27° C. in July and August down to 10° C. in January, whereas at Beaufort, only 10 miles west of Cape Lookout but inside the bar, the temperatures in December and January of 1930 were below 7° C. (Parr 1933: 57–58). In July of 1941 the water temperature ranged as high as 30° C., and the mean for the month was 28° C. The mean temperature in February 1942 was 5.5°, with temperatures as low as 2° being recorded (McDougall 1943: 331). Thus, the offshore bar serves to increase the annual temperature range in the sounds. Winter temperatures are lower than outside the bar because the effects of local cooling are not nullified by free mixing with the water in the open Atlantic. Parr (1933: 50, 53) placed the inner margin of the Gulf Stream between 20 and 25 land miles from the Cape Lookout Lighthouse, and mixing along the margins of the stream has a marked influence on the water along the coast south of Cape Hatteras. It is conceivable that the latitudinal range of certain of the Boreal species is extended further southward because of the protecting bars along the Carolina coast, but unfortunately it was not possible to reach favorable collecting sites on the outer edge of the bar to determine whether or not the halacarid fauna differs from that found inside. It is possible that Long Island likewise permits a southward extension of the ranges of one or two species in Long Island Sound, for the mean temperature in the Sound is lower than that outside. However, the North Carolina coast is a much more critical point in the range of the northern fauna, and the influence of the offshore bar should be more marked than that of Long Island.

The extremely small number of species found at Solomon's Island, Maryland, can be attributed largely to the low salinity which is normally 10–12 °/₀₀ and is occasionally much less at such times when the Patuxent River is bringing in large quantities of fresh water. Further studies would undoubtedly reveal a greater number of species toward the entrance of Chesapeake Bay and on the Atlantic coast of Delaware, but even there the fauna probably would not be as rich as that in Long Island Sound, since it is unlikely that the southward decline of the Halacaridae occurs at any one point along the coast (Cape Hatteras).

The fauna north of Connecticut appears to be relatively uniform as far as New Brunswick, since the total number of species taken in New Brunswick is not appreciably less than would be found in an equal number of samples from Long Island Sound. One species, *Rhombognathides merrimani*, with its two varieties, is found only in New Brunswick. *Rhombognathides pascens* and *seahami*, which appear together at Woods Hole, Massachusetts, are not found in the St. Andrews collections; and of these, only *R. pascens* is found in Long Island Sound. It is significant that there are as many species in 12 intertidal samples from St. Andrews as in the 26 carefully selected samples from intertidal and subtidal habitats in Beaufort. *Rhombognathides*, *Isobactrus*, *Thalassarachna* and *Arhodeoporus* reach their maximum development in the region between Connecticut and New Brunswick. *Copidognathus* s. str., on the other hand, is represented by only two species, as contrasted with the 10 which were found on two small bunches of *Halimeda* from Florida.

The small number of species known from Greenland and Labrador does not permit any comparison with the regions further to the south.

RELATIONSHIP OF THE NORTH AMERICAN FAUNA TO THE WORLD FAUNA

As is true in so many animal groups, the zoogeography of the Halacaridae is obscured by two important facts. In the first place earlier writers failed to note the relationship between closely related species from the various zoogeographic regions of the earth, and in the second place species have been compared with only remotely related species on superficial characters (*e. g.*, the common possession of heavy armor, or distinct panelling, or the absence of pectens on the claws) while fundamental and irreconcilable differences have been overlooked. Consequently, published descriptions of even closely related species (since the descriptions were usually incomplete) have often directed attention to entirely different characters so that it has been impossible for subsequent workers to make direct comparisons or contrasts between species. The most satisfactory work on the Halacaridae has been done by Lohmann and Viets, their descriptions and figures having been sufficiently detailed and accurate in most cases to permit other workers to recognize their species easily, but most important is the fact that their descriptions usually permit one to draw accurate conclusions as to the relationship or lack of relationship between species from different parts of the world.

The Halacaridae are an extremely important family from an ecological and zoogeographic standpoint, for there are few groups of microscopic animals which possess such a fortunate variety and number of morphological characters. Accordingly, it is usually possible to distinguish between fundamental and superficial differences and therefore to detect natural species groups within genera. The ease with which most of the Halacaridae can be transported from one place to another on floating seaweed, wood, *etc.*, makes it possible to mark the limits of the ranges of the various species with considerable certainty, for if a particular species is absent from a region it is usually because that species cannot live there, or because it cannot tolerate the conditions in the regions through which it would have to pass to get there. Hence the littoral Halacaridae should be of considerable value in establishing natural zoogeographic boundary zones when more extensive faunistic studies are available from parts of the world other than those which have now been studied. At the present time our knowledge of the Halacaridae of the world is rather meager, for only the North Atlantic, Caribbean, Mediterranean and Antarctic areas have been very extensively studied, while the Pacific Ocean has hardly been touched.

In Table II the fauna of North America has been compared with that of other parts of the earth, the comparison having been based not simply upon species common to the various regions, but also upon closely related species. Those species which, in the opinion of the writer, are immediately related to North American species, but which have not been found on this continent, are placed directly under their North American relatives and are indented. These include only the cases where direct relationship is virtually indisputable, all questionable relatives having been omitted.

Preliminary to a discussion of the relationship of the North American halacarid fauna to those faunae of other parts of the world, let us consider briefly the general aspects of distribution of marine littoral faunae. Ekman (1935) divided the littoral into a number of zoogeographic regions, the limits of which are marked by significant, but rarely abrupt, changes in the fauna. Fig. 331 shows those regions which are of greatest importance in the present discussion. The extent of the various regions is conditioned primarily by surface water temperature and therefore is influenced greatly by currents. Widely separated littoral regions, even if they have virtually identical thermal charac-

TABLE II. RELATIONSHIP OF THE NORTH AMERICAN FAUNA TO THE WORLD FAUNA. SEE TEXT, P. 196

	Ascension I.	*NE. S. America*	*Caribbean Sea*	*S. Florida*	*Bermudas*	*Cape Verde*	*Canary Is.*	*Azores*	*Mediterranean Sea*	*N. Adriatic Sea*	*Black Sea*	*SE. Australia*	*Macquarie Is.*	*Kerguelen I.*	*Antarctic Ocean*	*North Carolina*	*Chesapeake Bay*	*Conn.-Rhode Island*	*Massachusetts*	*Maine*	*New Brunswick*	*Labrador*	*Greenland*	*French Atlantic*	*British Isles*	*North Sea*	*Baltic Sea*	*Arctic Ocean*
Rhombognathus	.	.	+	+	.	.	.	.	+	+	+	.	+	.	+	+	+	.	.	.	.	.	+	+	+	+	+	+
magnirostris magnirostris	.	.	.	+	.	.	.	.	+	+	+	.	.	.	.	.	+	.	.	.	.	.	.	.	+	+	.	.
magnirostris lionyx	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	+	.	.	.	.	.	.	.	.	+	+	+	+
notops	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	.
Rhombognathides	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	+	.	+	.	.	+	+	+	+	.
pascens	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	+	.	.	.	.	+	+	+	+	.
seahami	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	+	.
mucronatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	+	+	+	.	.
merrimani merrimani	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
merrimani needleri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Metarhombognathus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	+	.	.	.	.	+	.	+
armatus americanus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	+	.	.	.	.	.	.	.
armatus armatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Isobactrus	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	+	+	+	+	.
setosus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	+	+	+	.
levis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.
hutchinsoni	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Halacarus s. str.	.	.	.	+	+	+	.	.	+	+	+	+	.	+	+	+	+	+	.	.	.	.	.	+	+	+	+	+
ctenopus	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.
subtilis	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
oblongus	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
actenos	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.
actenos robusta	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
frontiporus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
anomalus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	+	+	+	.

TABLE II. RELATIONSHIP OF THE NORTH AMERICAN FAUNA TO THE WORLD FAUNA. SEE TEXT, P. 196 (*cont.*)

	Ascension I.	*NE. S. America*	*Caribbean Sea*	*S. Florida*	*Bermudas*	*Cape Verde*	*Canary Is.*	*Azores*	*Mediterranean Sea*	*N. Adriatic Sea*	*Black Sea*	*SE. Australia*	*Macquarie Is.*	*Kerguelen I.*	*Antarctic Ocean*	*North Carolina*	*Chesapeake Bay*	*Conn.-Rhode Island*	*Massachusetts*	*Maine*	*New Brunswick*	*Labrador*	*Greenland*	*French Atlantic*	*British Isles*	*North Sea*	*Baltic Sea*	*Arctic Ocean*
H. (Thalassarachna)	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	+	.	.	+	.	+	+	+	+	+	+
basteri basteri	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	+	+	.	+	+	+	+	+	+
b. septentrionalis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
b. affinis	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
longipes	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	+	+	.
balticus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	+	.	+	+	.
capucinus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	+	.
procerus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.
subterraneus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	+	.
Agaue	.	+	.	+	+	+	+	+	+	+	+	+	+	.	+	.	.	.	.	.	.	.	.	+	+	.	.	+
nationalis	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
adriatica	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Copidognathus **s. str.**	+	+	+	+	+	+	.	+	+	+	+	+	+	+	+	+	.	+	.	.	.	+	.	+	+	+	+	+
punctatissimus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.
acutus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
latus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
bairdi	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
gibberipes	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
curassaviensis	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
biscayneus	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
angustus floridensis	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
angustus angustus	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
lamellosus	.	+	.	.	+	.	.	.	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
septentrionalis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.
poucheti	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
gracilis	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

TABLE II. RELATIONSHIP OF THE NORTH AMERICAN FAUNA TO THE WORLD FAUNA. SEE TEXT, P. 196 (*cont.*)

	Ascension I.	*NE. S. America*	*Caribbean Sea*	*S. Florida*	*Bermudas*	*Cape Verde*	*Canary Is.*	*Azores*	*Mediterranean Sea*	*N. Adriatic Sea*	*Black Sea*	*SE. Australia*	*Macquarie Is.*	*Kerguelen I.*	*Antarctic Ocean*	*North Carolina*	*Chesapeake Bay*	*Conn.-Rhode Island*	*Massachusetts*	*Maine*	*New Brunswick*	*Labrador*	*Greenland*	*French Atlantic*	*British Isles*	*North Sea*	*Baltic Sea*	*Arctic Ocean*
hummelincki	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
adriatica	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tricorneata	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
caudatus	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
pulcher	+	.	.	+	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
triops	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
magnipalpus magnipalpus	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
magnipalpus serratisetus	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
magnipalpus ponticus	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
pachypus	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
extensus	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
bonairensis	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
C. (Arhodeoporus)	.	.	.	.	.	.	.	+	+	+	+	.	.	.	.	+	.	+	+	.	.	.	.	+	+	+	.	.
arenarius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.
gracilipes s. lat.	.	.	.	.	.	.	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.
submarinus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Agauopsis	.	+	.	+	+	+	+	+	+	+	+	+	.	+	+	+	+	+	.	.	.	.	.	+	+	.	.	.
brevipalpus brevipalpus	.	+	.	+	+	.	+	+	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.
brevipalpus pontica	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
borealis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.
Lohmannella	.	.	.	.	.	.	.	+	+	.	+	.	.	+	+	.	.	+	.	.	+	.	.	+	+	+	+	.
falcata	.	.	.	.	.	.	.	.	+	.	+	.	.	+	+	.	.	+	.	.	+	.	.	+	+	+	+	.

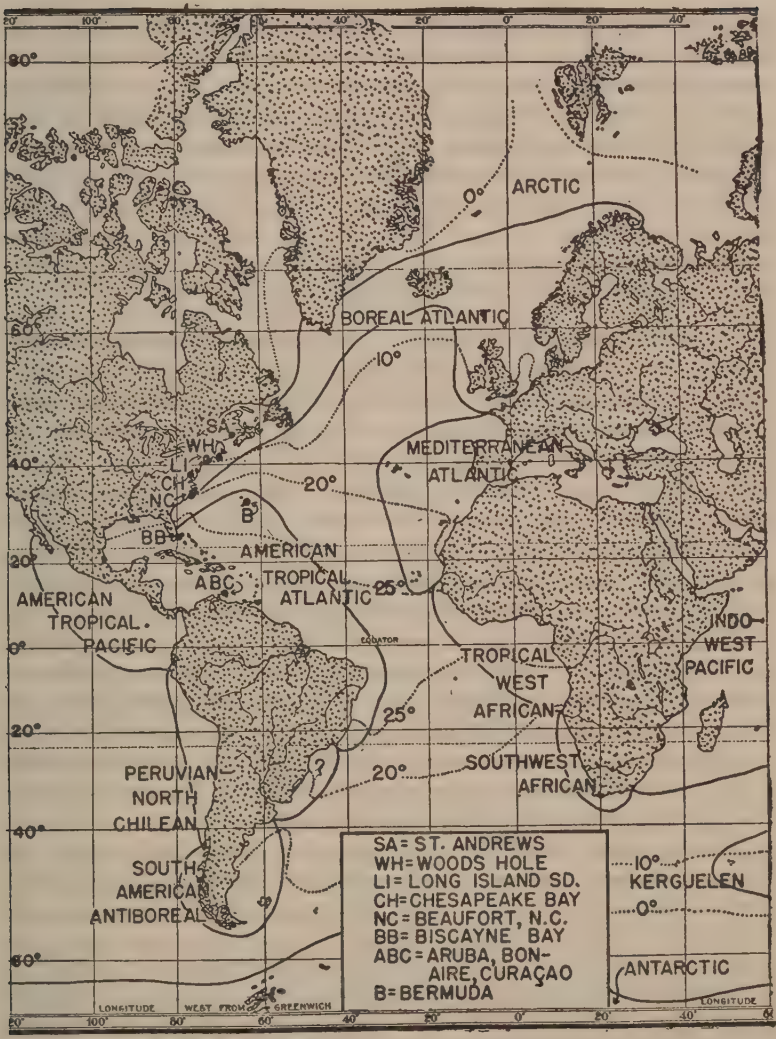
ARCTIC
0°
BOREAL ATLANTIC
10°
SA
WH
LI
CH
NC
BB
B
20°
MEDITERRANEAN ATLANTIC
AMERICAN TROPICAL ATLANTIC
ABC
25°
AMERICAN TROPICAL PACIFIC
EQUATOR
TROPICAL WEST AFRICAN
INDO-WEST PACIFIC
25°
PERUVIAN NORTH CHILEAN
20°
SOUTHWEST AFRICAN
SOUTH AMERICAN ANTIBOREAL
SA = ST. ANDREWS
WH = WOODS HOLE
LI = LONG ISLAND SD.
CH = CHESAPEAKE BAY
NC = BEAUFORT, N.C.
BB = BISCAYNE BAY
ABC = ARUBA, BONAIRE, CURAÇAO
B = BERMUDA
10°
KERGUELEN
0°
ANTARCTIC
LONGITUDE WEST FROM GREENWICH
LONGITUDE
80°
60°
40°
20°
0°
20°
40°
60°
100°
80°
60°
40°
20°
0°
20°
40°

Figure 331. Ekman's zoogeographic regions, based on Ekman (1935) and on Sverdrup, Johnson and Fleming (1942: 804). The principal points of study in the western hemisphere are also included. The Bermuda fauna is known through the work of Lohmann (1893a); that of Aruba, Bonaire and Curaçao through the work of Viets (1936d). The dotted lines indicate the mean annual position of the 25°, 20°, 10° and 0° C. isotherms according to Schott (1926) and Sverdrup, Johnson and Fleming (1942).

teristics, usually differ faunistically because of land, abyssal or temperature barriers, or because oceanic currents may be such as to prevent the free dispersal of the members of the faunae. Historical factors are also of prime importance in the development of similarities or differences between faunae. The Atlantic coast of North America lies within three faunistic regions: the Arctic region extending approximately to northern Newfoundland, the Boreal Atlantic region extending approximately to Cape Hatteras, and the American Tropical Atlantic region which includes southern Florida, Bermuda, the Caribbean Sea, and reaches to the southeastern coast of Brazil.

American Boreal Atlantic Fauna. The fauna of the American Boreal Atlantic has a close affinity with that of the European Boreal region. Of the 25 American Boreal forms listed in Table II, 15 (60%) are found in the European Boreal region, two (8%) are closely related to European forms but not identical, and eight (32%) are endemic. Therefore, nearly 70 per cent of the American forms are identical with, or closely related to, European Halacaridae. Schulz (1935a: 87) listed a total of 41 forms from the North Sea and Baltic combined. Of these, 36 forms are known from the North Sea, but five[23] are of questionable validity, leaving a total of 31 forms known from the North Sea as compared with 25 from the American Boreal Atlantic. But in addition, Shulz listed 24 forms from the Baltic, five of which are not known from the North Sea, making a total of 36 forms from the Baltic and North Sea. These combined make up the present known halacarid fauna from the European Boreal Atlantic. If one assumes the fauna of the American coast to be as extensive as that of Europe, then only about 70 per cent of our fauna has been discovered.

The American Boreal fauna shows very little affinity with the Tropical faunae, for only one species, the definitely eurythermal *Rhombognathus magnirostris*, with its two varieties, has been found in Tropical as well as in Boreal regions. On the European coast this species extends at least as far north as Bergen, Norway (about 60° 30′ N. latitude), whereas its northernmost limit on our coast is approximately between 38° and 41° N. latitude, judging from our present knowledge.

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[23] Schulz 1935a, 87: ". . . 8. *Rhombognathides pascens* nov. var., . . . 10. *Rhombognathopsis minutus*, . . . 24. *Halacarellus capucinus*, . . . 27. *Halacarellus floridearum* nov. var., . . . 36. *Copidognathus* spec. . . . " The latter is evidently *Halacarus* sp.? (Larve) Lohmann 1893.

A slightly greater affinity is seen between the American Boreal and the Mediterranean-Atlantic. Five of the 25 American forms are either identical (two varieties of *R. magnirostris; Lohmannella falcata*) with Mediterranean forms, or have close relatives there (*Halacarus* (*Thalassarachna*) *basteri basteri, Copidognathus* (*Arhodeoporus*) *arenarius*). This is not surprising in view of the fact that many Mediterranean animals extend far into the European Boreal, and some even reach into the Arctic.

Transition Zone. Ekman designated the region between Cape Hatteras and southern Florida as a transition zone. As pointed out on page 194, its transitional nature consists not so much of an overlapping of Tropical and Boreal faunae as it does of the dropping out of certain of the Boreal genera or subgenera. The one endemic species found at Beaufort has its closest relative in *C. latus*, a North Sea form, so that it can be considered a Boreal rather than a Tropical species. The short distance separating the American Boreal from the American Tropical region contrasts sharply with the great distance between the European Boreal and the Tropical West African. It seems unlikely that there is room enough for the development of an endemic fauna in the transitional zone from Cape Hatteras to Florida, and therefore it is probable that future work will show that this portion of the coast is occupied by a fauna comprising largely the most eurythermal species of the Tropical and Boreal faunae. The great annual latitudinal shifts of the isotherms in this region would wipe out any species with restricted temperature requirements, and for this reason the Mediterranean Atlantic fauna has no real counterpart on the eastern coast of North America. This is due to the convergence of the isotherms on the North American coast in contrast with their divergence on the European-African coast, which in turn is due to the influence of the North Atlantic and Labrador Currents.

American Tropical Atlantic Fauna. The Florida fauna is clearly tropical in character. It has been pointed out (see p. 194) that there is no correlation between the Florida and the American Boreal faunae, except through the eurythermal *Rhombognathus magnirostris;* but there is a close affinity between the faunae of the Dutch West Indies, southern Florida and Bermuda, all of which lie within Ekman's American Tropical Atlantic region. Of the 15 forms known from Florida, four are also found in the Dutch West Indies, and at least three others are clearly related to Dutch West Indies species. Thus, seven (32%) of the 22 species known from both the Dutch West Indies and Florida are either common to the two or are represented by closely related forms, and it is most likely that further collection from the Caribbean Sea and Florida will show even greater homogeneity in this region. Lohmann (1893a) listed seven species from Bermuda, five of which are represented in the Florida fauna, four being identical and another closely related to a Florida species.

The Halacaridae of the Tropical West African fauna are unknown, hence a comparison with the American Tropical Atlantic cannot be made at this time. But the work of Viets (1939c, 1940g), who listed a total of 54 forms from the Mediterranean, Adriatic and Black Seas, makes possible a comparison with the Mediterranean fauna. Viets listed 28 forms from the Mediterranean, two of which are identical with and two closely related (total 14%) to forms from the American Tropical Atlantic. Viets also listed 34 forms from the northern Adriatic, and eleven (32%) of these are either identical with (3), or closely related to (8), American Tropical Atlantic forms. Sixteen forms are known from the Black Sea, of which five (31%) are near (3), or identical with (2), Tropical American forms.

Tethyian fauna. Note that five of the 15 Florida species are either identical with species from both the Mediterranean and from southeastern Australia, or are members of species groups which occupy this wide range. This is of particular interest in connection with the Tethys Sea which was in existence throughout the Mesozoic and the early Cenozoic. Although this sea varied considerably in extent and form during this period, it maintained a virtually uninterrupted marine connection between the western Pacific and what is now the Caribbean. The mild climates which prevailed were at least partly due to the disposition of the land masses, which more or less restricted the interchange of water between the Tropical and Arctic seas, and as a consequence the entire Tethys Sea was tropical, supporting one of the richest marine faunae of all time. This fauna was relatively uniform throughout its entire extent until the extensive mountain-building and general continental emergence of the Tertiary broke up the Tethys Sea into a number of isolated basins, namely the Caribbean, Mediterranean, Black and Caspian Seas, and the Indo-West Pacific Ocean. The fate of the Tethys fauna with which the present day remnants of this ancient sea were once uniformly endowed has depended upon the subsequent history of the remnants. The Caribbean and Indo-West Pacific regions have remained tropical in character and have maintained their Tethyian fauna most successfully. The Mediterranean, Black and Caspian Seas, because of interrelated geographical and climatological changes, have lost their tropical fauna to a lesser or greater degree. Of these the Mediterranean fauna most closely approaches that of the Tropical seas, whereas the Caspian fauna shows the greatest change. When the Halacaridae of the Pacific and Indian Oceans have been more extensively studied it is likely that they will augment the picture which has been created from a study of other animal groups.

DISTRIBUTION OF THE GENERA AND SUBGENERA

Table II shows that the absence of *Rhombognathides*, *Metarhombognathus*, *Isobactrus*, *Thalassarachna*, *Arhodeoporus* and *Lohmannella* from the Florida collections was no artifact, for representatives of these have never been recorded from Tropical regions. *Lohmannella* and *Arhodeoporus* are known from the Mediterranean, Adriatic and Black Seas; but *Rhombognathides*, *Metarhombognathus* and *Isobactrus* are characteristically Boreal or Arctic in their ranges.[24] *Rhombognathides* is found in the Black Sea, which, despite its Tethyian ancestry, has a fauna containing a number of species of Arctic or Boreal origin.

The other genera or subgenera are less restricted in their ranges. *Rhombognathus*, *Halacarus* s. str., *Agaue*, *Copidognathus* s. str. and *Agauopsis* have been reported from both Antarctic and Tropical regions. The distribution of *Agauopsis* in the North Atlantic is of interest. Only two forms (*Agauopsis brevipalpus brevipalpus* and *A. microrhyncha minor*) are known from the European Atlantic Coast, but these have not been found north of Ireland or the English Channel. On the American coast *A. borealis* is found at least as far north as Long Island Sound, which is equivalent, zoogeographically, to Norwegian latitudes.

One of the most significant features of the Tropical fauna is the predominance of *Copidognathus* s. str. Ten of the 15 species (67%) taken in the Florida collections belong to this group. Of the 11 species which Viets (1936d) listed from the Dutch West Indies, nine (82%)

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[24] Trouessart (1900a; 1901c) listed *Rhombognathides trionyx* (Trt.) 1900 from Tierra del Fuego, and also from St. Guenole on the French coast. This is the only record of *Rhombognathides* outside the northern hemisphere.

were *Copidognathus* s. str. species. In the Mediterranean-Black Sea region the predominance is less marked. Only 24 of the 54 species (45%) listed from there (Viets, 1940g) belong to the subgenus. Of the 36 certain species from the European Boreal Atlantic (Schulz, 1935a), only six (16%) are *Copidognathus* s. str. species, and in the American Boreal Atlantic, the proportion is of the same order of magnitude (3/25 = 12%). Four of the 23 species (17%) of Halacaridae now known from the Antarctic region are *Copidognathus* s. str. species (Viets, 1931f: 8).

THE STRUCTURE OF LOCAL FAUNAE

As pointed out in the previous two sections, the subdivisions of the halacarid fauna of our coast follow in general the zoogeographic subdivisions outlined by Ekman (1935), and these in turn are determined largely by temperature; but in any one locality temperature appears to be of little direct significance in determining the structure of the fauna within the numerous special habitats. Exceptions to this generalization are probably numerous, but most of them would be of an extremely local nature and would not affect an appreciable portion of the population. Significant exceptions may be demonstrable along the North Carolina coast and in similar situations where offshore bars result in markedly different temperatures within small areas, but under usual conditions such factors as tides, substrate and salinity play the major roles in determining the structure of the fauna of any given locality.

The Subtidal Fauna

The collections which have been made from subtidal habitats in Long Island Sound indicate a relatively uniform halacarid fauna as compared with that of the intertidal zone. Although differences in abundance do occur in the former the sharp qualitative differences which are seen between the various intertidal habitats do not appear in the subtidal zone, due to the more uniform distribution of food, which consists principally of copepods and ostracods in the case of most of the subtidal Halacaridae. The Rhombognathinae are restricted to algal food, but as will be seen later, many of these are excluded from the subtidal zone by factors other than food.

Tables III and VII show that the dominant species are *Copidognathus* (*Arhodeoporus*) *arenarius* and *C.* (s. str.) *septentrionalis*. The predominance of the first of these is probably more marked than the

TABLE III. NUMBERS OF HALACARIDAE OBTAINED FROM VARIOUS MATERIALS DREDGED FROM LONG ISLAND SOUND

Sample No.	*Locality*	*Depth (m.)*	*Substrate*	*Date*	*Species*										
					Rhombognathides pascens	*Halacarus (s. str.) frontiporus*	*Halacarus (s. str.) anomalus*	*H. (Thalassarachna) basteri basteri*	*H. (Thalassarachna) longipes*	*Copidognathus (s. str.) punctatissimus*	*Copidognathus (s. str.) septentrionalis*	*C. (Arhodeoporus) arenarius*	*C. (Arhodeoporus) submarinus*	*Lohmannella falcata*	*Total Halacaridae*
44–71	Off Stratford Point, Conn.	16	*Ostrea;* 7; av. length 8.2 cm.	July 14, 1944	—	—	3	—	—	5	1320	380	—	2	1710
44–72	About 2 mi. s. of Momauguin, Conn.	10	*Ostrea;* 1; 18 cm. long	July 14, 1944	—	—	—	—	—	24	—	36	—	—	60
44–73	About 2 mi. s. of Momauguin, Conn.	10	*Suberites;* ca. 9 cm. in diameter	July 14, 1944	—	—	—	—	—	1	—	20	—	—	21
44–74	Off Mansfield Point, Conn.	3.5	*Laminaria;* 50 g.	Aug. 4, 1944	—	—	—	—	—	—	—	—	—	—	0
44–75	Off Mansfield Point, Conn.	3.5	*Laminaria* overgrown with *Sertularia;* 52 g.	Aug. 4, 1944	2	—	—	1	—	11	4	16	—	—	34
44–78	Off Mansfield Point, Conn.	3.5	Filamentous red algae; 5.8 g.	Aug. 4, 1944	1	—	—	2	2	2	—	11	—	—	18
44–79	Off Mansfield Point, Conn.	3.5	Filamentous green algae; 2.5 g.	Aug. 4, 1944	—	—	—	5	2	6	5	2	—	—	20
44–80	Off Mansfield Point, Conn.	3.5	Detached *Fucus;* 14.7 g.	Aug. 4, 1944	—	—	—	1	—	—	3	7	—	—	11
44–81	New Haven Harbor, between Lighthouse Point and Morris Cove	3 to 4	Empty *Ostrea* valves extensively pitted by *Cliona;* 5; av. length 9.5 cm.	Aug. 4, 1944	—	—	—	—	2	12	13	487	—	—	514
45–1	New Haven Harbor, on west side of channel	3 to 6	Broken *Ostrea* valves	Jan. 4, 1945	—	—	—	—	—	4	56	860	—	—	920
44–82	About 3 mi. ne. of Block Island, Rhode Island	41	*Laminaria* overgrown with *Sertularia*	Aug. 13, 1944	8	11	—	—	—	—	4	—	26	2	51
				Totals	11	11	3	9	6	65	1405	1819	26	4	3359

totals in Table VII indicate, for most of the specimens of *C. septentrionalis* were obtained in a single sample, but *C. arenarius* appeared more frequently and usually in greater numbers. *C. arenarius* extends into the intertidal area as well, where it becomes an arenicolous form, but *C. septentrionalis* does not, only one individual having been taken there.

C. (s. str.) *punctatissimus* is the third most abundant species in the subtidal zone. Like *C. arenarius* it also ranges into the intertidal zone, but unlike the latter it is not a very successful arenicolous species, possibly owing to its unfavorable form. Although both species are of approximately the same length, the body of *C. punctatissimus* is 0.66 as broad as long, whereas that of *C. arenarius* is only about 0.56 as broad as long. In the other arenicolous forms most individuals have a body less than 0.60 as broad as long, and in *Halacarus* (s. str.) *anomalus* the ratio of width to length is about 0.45.

Halacarus (*Thalassarachna*) *longipes* and *Lohmannella falcata* are typically subtidal, but they are much less abundant than the other forms. *Halacarus* (*Thalassarachna*) *basteri basteri* appears both above and below the low tide zone. Although *Halacarus* (s. str.) *anomalus* has been taken in one subtidal collection, it is a typical arenicolous form. The presence of *Rhombognathides pascens* below the intertidal is seemingly a natural occurrence, for it has been taken on at least three occasions, living specimens having been found each time. Viets (1927a: 166) also showed both *Rhombognathides pascens* and *seahami* to be present in most samples which he took below the tide zone in the North Sea. The complete absence of *Metarhombognathus* and *Isobactrus* from subtidal collections is significant, for Viets (1927a: 160–161, 166) showed a similar distribution of these two intertidal genera in his North Sea collections. (For further discussion, see p. 216). *Halacarus* (*Thalassarachna*) *balticus*, *capuzinus* and *subterraneus* are absent from the subtidal zone and are typically intertidal forms. Limited collections somewhat beyond the eastern end of Long Island Sound indicate the development of a rather different fauna at depths of 40 meters, suggesting a transition from a eulittoral to a sublittoral fauna. Two new species appear here, *Halacarus* (s. str.) *frontiporus*, and *Copidognathus* (*Arhodeoporus*) *submarinus*. The former is clearly a sublittoral type, being weakly armored and having a soft cuticle; the dorsal plates are not recognizable as distinct sclerites and the corneae are highly modified. *Copidognathus* (*Arhodeoporus*) *submarinus* replaces *arenarius* which is found in shallower water. *Rhombognathides pascens* is also found here.

The Intertidal Fauna

In contrast with the relatively uniform halacarid fauna in the subtidal zone, the intertidal zone of Long Island Sound is characterized by a number of distinct faunae showing a close correlation with the substrate upon which they are developed. In this area there are numerous sandy beaches and usually there is sand of sufficient particle size to permit the development of a typical arenicolous fauna. Exposed rocks provide attachment places for *Fucus*, *Chondrus*, *Ascophyllum* and other algae, as well as for *Mytilus*, *Modiolus* and *Ostrea*. Patches of salt grass and mud flats often support algae which may be used as food by the Rhombognathinae, or these may support populations of other microscopic animals which are preyed upon by the Halacarinae and other predaceous groups. Because of the diversity of the faunae of the intertidal zone, the principal ones will be considered separately, these being the faunae of the sand, molluscs and algae.

Intertidal Sand Fauna. The intertidal sand fauna contains three species which are rarely found in other habitats, and in addition *Copidognathus* (*Arhodeoporus*) *arenarius*, which is typically a subtidal form, appears consistently and often in appreciable numbers in the intertidal, especially in the low tide zone. As can be seen in Table IV, *Copidognathus arenarius* is found at considerable depths in the beach, and therefore it can be considered a truly arenicolous species rather than a psammoxene form whose frequent appearance in the intertidal is due simply to its abundance in the subtidal zone.

The species which are most characteristically arenicolous are: *Halacarus* (s. str.) *anomalus*, *Halacarus* (*Thalassarachna*) *capuzinus* and *Halacarus* (*Thalassarachna*) *subterraneus*. *Halacarus anomalus* is well adapted to its arenicolous environment, its body being cylindrical in form, more than twice as long as broad, and flexible, the last being a unique character among the Halacaridae. The long slender legs, the third and fourth pairs of which are displaced far posteriorly, enable the mite to move through sand with considerable ease either forward or backward, whereas on a glass surface it is the most helpless and awkward of the Halacaridae seen by the writer. The two other species show less striking modifications, but both are unique in the possession of additional platelets in the membranous areas. *Halacarus capuzinus* has an unusually slender body for this subgenus (L/W = 1.8–2.0), whereas *Halacarus subterraneus* is not especially narrowed, although it is noticeably flatter than most species. Generally, the appearance of Rhombognathinae in sand samples is fortuitous, the mites probably having been dislodged from their normal substrate. The finding of more specimens of *Rhombognathides mucronatus* in sand than on other substrates is almost certainly an artifact, for *Rhombognathides* is an algicolous genus, and these were taken in clean sand. *Isobactrus setosus*, because of its small size, may be able to live at limited depths in the sand, but most individuals found there probably are to be considered as psammoxene forms. In the latter category are also *Halacarus* (*Thalassarachna*) *basteri basteri* and *Copidognathus* (s. str.) *septentrionalis*. In locations where sand has been overgrown with salt grass, which effectively reduces the impact of the water upon the sand, there may develop an atypical sand fauna which includes Rhombognathinae and other forms generally found in association with *Balanus* due to the growth of filamentous green algae over the surface of the sand. *Metarhombognathus armatus americanus* is often found in considerable numbers in such situations, as is shown in Table XI (sample 44–85). The same situation is common in Long Island Sound.

The Halacaridae found in sand may be classified as follows:

Psammobiont.
  Halacarus (s. str.) *anomalus*.
  Halacarus (*Thalassarachna*) *capuzinus*.
  Halacarus (*Thalassarachna*) *subterraneus*.

Psammophile.
  Copidognathus (*Arhodeoporus*) *arenarius*.

Psammoxene.
  Rhombognathinae.
  Halacarus (*Thalassarachna*) *basteri basteri*.
  Copidognathus (s. str.) *punctatissimus*.
  Copidognathus (s. str.) *septentrionalis*.

There is a close similarity between the sand fauna of the American Boreal Atlantic and that of the European Boreal, since all three of the above psammobiont species are common to the two regions. Schulz (1933, 1935a) has listed them as members of the coastal ground-water fauna. However, *Copidognathus* (*Arhodeoporus*) *gracilipes* has not been shown to occupy a position homologous with that of *Copido-*

TABLE IV. NUMBERS OF HALACARIDAE OBTAINED FROM INTERTIDAL SAND SAMPLES, LONG ISLAND SOUND, NEW HAVEN COUNTY, CONNECTICUT; ALL 500 CC. SAMPLES

Locality and Date	*Sample No.*	*Tide Zone*	*Depth (cm.)*	*Species*											
				Rhombognathides mucronatus	*Metarhombognathus armatus americanus*	*Isobactrus setosus*	*Isobactrus hutchinsoni*	*Halacarus (s. str.) anomalus*	*H. (Thalassarachna) basteri basteri*	*H. (Thalassarachna) capuzinus*	*H. (Thalassarachna) subterraneus*	*Copidognathus (s. str.) punctatissimus*	*Copidognathus (s. str.) septentrionalis*	*C. (Arhodeoporus) arenarius*	*Total Halacaridae*
Morris Cove, March 22–29, 1944	44–1	Low	0 to 1	—	1	4	—	—	—	—	—	—	—	2	7
	44–15	Low	0 to 1	—	—	3	—	—	—	—	—	—	—	—	3
	44–16	Mid	0 to 1	—	—	5	—	—	—	—	—	—	—	—	5
	44–3	Mid	10	—	—	1	—	219	—	1	53	—	—	5	279
	44–87	High	0 to 1	—	—	2	—	—	—	—	—	—	—	—	2
	44–9	High	0 to 1	—	—	1	—	—	—	—	—	—	—	—	1
	44–10	High	30	—	—	—	—	20	—	—	11	—	—	—	31
	44–2	High	50	—	—	—	—	35	—	—	7	—	—	—	42
South End, April 7, 1944	44–22	Low	0 to 1	—	—	—	—	—	—	—	—	—	—	—	0
	44–23	Low	5	—	—	—	4	—	—	2	—	—	—	13	19
	44–24	Low	0 to 4	—	—	—	—	—	—	—	3	—	—	—	3
	44–25	Low	5 to 10	—	—	—	—	1	—	—	—	—	—	2	3
	44–26	Mid	0 to 4	—	—	—	—	—	—	—	—		—	—	0
	44–27	Mid	30 to 35	—	—	—	—	2	—	—	—	—	—	2	4
	44–28	High	0 to 5	—	—	—	—	—	—	—	—	—	—	—	0
	44–29	High	55 to 60	—	—	—	—	3	—	—	—	—	—	—	3
Double Beach, Oct. 13, 1943	43–43	Low	0 to 5	4	—	—	—	—	—	—	—	—	1	14	19
	43–51	Low	0 to 10	—	—	—	—	—	—	—	—	11	—	128	139
	43–44	Mid	0 to 1	10	2	12	—	—	3	—	—	—	—	42	69
	43–50	High	?	16	—	2	—	—	—	30	—	—	—	—	48
			Totals:	30	3	30	4	280	3	33	74	11	1	208	677

gnathus (*Arhodeoporus*) *arenarius*, and if it does not, this may be in part attributable to its greater size.

Intertidal Molluscan Fauna. Three molluscs in particular provide a substrate for the development of halacarid faunae, namely *Mytilus*, *Modiolus* and *Ostrea*, of which the *Mytilus* fauna is the simplest. Because the byssal threads often provide attachment for filamentous green algae, the fauna is probably a self-sustaining one and not dependent upon repeated introductions from surrounding habitats. Note in Table V that the dominant forms are also the principal psammoxene species. Since the matted byssal threads usually contain sand, it is not surprising that certain psammobiont or psammophile species occasionally appear.

The ribbed surface of *Modiolus* is somewhat more suitable for the development of a typical fauna than the relatively smooth surface of *Mytilus*, but more important, it provides an excellent attachment place for *Balanus*. The resulting surface contains many crevices in which *Isobactrus setosus* and *Metarhombognathus armatus americanus* can find secure footing and a certain amount of protection from Amphipoda and other enemies. *Balanus*-encrusted surfaces usually support a moderately heavy growth of unicellular or filamentous algae. The fact that the dominant species are algicolous demonstrates that the algae are really the most important part of this association so far as the Halacaridae are concerned.

The significance of the encrustation of *Modiolus* by *Balanus* can be seen by comparing sample 44–4 (unencrusted) with 44–5, 43–28 and 43–30 (Table V). Three samples of encrusted molluscs contain only 2.5 times as many *Modiolus* as sample 44–4, but 27 times as many mites. *Halacarus* (*Thalassarachna*) *balticus* is a characteristic species of this fauna, for its large size prohibits its living in the sand, and although it seemingly is not restricted to intertidal habitats, it is not common below the low tide zone (Table VII of this paper; also Viets 1927a: 161, 166). The two species of Rhombognathinae with which it lives probably form a principal part of its diet, for the writer has seen it feeding upon these species on numerous occasions in laboratory cultures. The halacarid fauna developed upon *Ostrea* in the intertidal zone is essentially like that of *Modiolus* and *Balanus*.

Algicolous Fauna. The halacarid faunae developed on intertidal algae are dominated by the Rhombognathinae. Of the 309 mites

TABLE V. NUMBERS OF HALACARIDAE OBTAINED FROM INTERTIDAL MOLLUSCA AT NEW HAVEN, CONNECTICUT

Sample No.	Locality, Date	Substrate	Number	Av. Length (cm.)	Species								
					Rhombognathides mucronatus	*Metarhombognathus armatus americanus*	*Isobactrus setosus*	*Isobactrus hutchinsoni*	*Halacarus (Thalassarachna) balticus*	*Halacarus (Thalassarachna) subterraneus*	*Copidognathus* (s. str.) *punctatissimus*	*Copidognathus (Arhodeoporus) arenarius*	*Total Halacaridae*
44–7	Morris Cove, March 29, 1944	*Mytilus*	10	5.1	—	—	9	—	—	1	—	—	10
44–6	Morris Cove, March 29, 1944	*Mytilus*	11	4.8	—	—	16	—	—	1	—	—	17
44–32	Lighthouse Point, April 19, 1944	*Mytilus*	4	5.5	—	10	5	1	—	—	—	1	17
43–28	Morris Cove, June 11, 1943	*Modiolus* encrusted with *Balanus*	10	?	—	88	48	—	2	1	—	1	140
43–30	Morris Cove, June 25, 1943	*Modiolus* encrusted with *Balanus*	6	?	9	65	150	—	31	—	—	2	257
44–5	Morris Cove, March 29, 1944	*Modiolus* encrusted with *Balanus*	8	6.6	—	209	149	—	19	—	1	—	378
44–4	Morris Cove, March 29, 1944	*Modiolus*, unencrusted	10	5.6	—	8	18	—	3	—	—	—	29
44–70	Fort Hale Park, June 3, 1944	*Modiolus* growing in non-tidal pool. Salinity 25.4°/₀₀	3	7.5	—	—	—	—	—	—	2	—	2

TABLE VI. NUMBERS OF HALACARIDAE OBTAINED FROM INTERTIDAL ALGAE IN LONG ISLAND SOUND; ALL FROM NEW HAVEN COUNTY, CONNECTICUT

Sample No.	*Locality, Date*	*Substrate*	*Weight (g.)*	*Tide Zone*	*Species*									
					Rhombognathides pascens	*Metarhombognathus armatus americanus*	*Isobactrus setosus*	*Isobactrus levis*	*Halacarus (Thalassarachna) basteri basteri*	*Halacarus (Thalassarachna) balticus*	*Copidognathus (s. str.) punctatissimus*	*Copidognathus (Arhodeoporus) arenarius*	*Agauopsis borealis*	*Total Halacaridae*
43–26	Morris Cove, June 11, 1943	*Enteromorpha*, mostly dead	50	High	—	150	5	—	—	1	—	—	2	158
43–37	Morris Cove, Oct. 9, 1943	*Enteromorpha*	40	Low	—	2	98	4	—	—	—	—	—	104
44–20	South End, Apr. 7, 1944	*Chondrus*	74	Low	10	—	—	—	—	—	—	—	—	10
44–21	South End, Apr. 7, 1944	*Ascophyllum*	153	Low	—	—	2	—	—	—	—	—	—	2
44–30	South End, Apr. 7, 1944	*Enteromorpha*	42	Mid	—	—	1	—	—	1	1	2	—	5
43–38	Double Beach, Oct. 13, 1943	*Ascophyllum*	70	Low	21	—	—	—	—	—	—	—	—	21
43–39	Double Beach, Oct. 13, 1943	*Polysiphonia*	17	Low	7	—	—	—	—	—	—	—	—	7
43–40	Double Beach, Oct. 13, 1943	*Chondrus*	50	Low	6	—	—	—	—	—	—	—	—	6
43–41	Double Beach, Oct. 13, 1943	*Chondrus*	60	Low	—	—	—	—	—	—	—	1	—	1
43–42	Double Beach, Oct. 13, 1943	*Ulva*	125		4	—	—	—	1	—	—	—	—	5

recorded in Table VI, all but nine, or about 97 per cent, are Rhombognathinae. None of the Halacarinae can be considered typical algicolous forms. One of the most interesting aspects of the local distribution of the Rhombognathinae is the absence of *Rhombognathides pascens* from collections made inside New Haven Harbor, although this species is found at South End, which is just a mile southeast of Morris Cove, but on the Sound. The reasons for this distribution are not clear, but it is probably related to the slightly lower salinities or the higher temperatures found inside the harbor. The dropping out of *Rhombognathides seahami* between Woods Hole and New Haven, and the total absence of *Rhombognathides* from the North Carolina collections, suggest that Long Island Sound may be near the southern limit of the range of the genus, in which case local distribution of the species may be considerably affected by slight local variations in temperatures. *Rhombognathides merrimani* is not known from Connecticut and may disappear even between New Brunswick and Cape Cod.

It was indicated above that the *Modiolus-Balanus* fauna is essentially an algicolous one, since the dominant species depend upon *Enteromorpha* and filamentous green algae growing on the *Balanus*. The addition of *Halacarus* (*Thalassarachna*) *balticus* is a refinement not found in strictly algicolous faunae, however, and for that reason the fauna must be considered distinct from those found on algae.

Table VII. Summary of General Collections in Long Island Sound

	Subtidal	*Intertidal*			*Totals*
		Sand	*Mollusca*	*Algae*	
Rhombognathides pascens	11	—	—	48	59
Rhombognathides mucronatus	—	30	9	—	39
Metarhombognathus armatus americanus	—	3	380	152	535
Isobactrus setosus	—	30	395	106	531
Isobactrus levis	—	—	—	4	4
Isobactrus hutchinsoni	—	4	1	—	5
Halacarus (s. str.) *anomalus*	3	280	—	—	283
Halacarus (s. str.) *frontiporus*	11	—	—	—	11
H. (*Thalassarachna*) *basteri basteri*	9	3	—	1	13
H. (*Thalassarachna*) *balticus*	—	—	55	2	57
H. (*Thalassarachna*) *capuzinus*	—	33	—	—	33
H. (*Thalassarachna*) *subterraneus*	—	74	3	—	77
H. (*Thalassarachna*) *longipes*	6	—	—	—	6
Copidognathus (s. str.) *punctatissimus*	61	11	3	1	76
Copidognathus (s. str.) *septentrionalis*	1405	1	—	—	1406
C. (*Arhodeoporus*) *arenarius*	1739	208	4	3	1954
C. (*Arhodeoporus*) *submarinus*	26	—	—	—	26
Agauopsis borealis	—	—	—	2	2
Lohmannella falcata	4	—	—	—	4
Total					5121

The Fauna of Nontidal Habitats in the Intertidal Zone

The writer has had the opportunity of studying two examples of a special type of habitat which reveal important facts in the ecology of certain Halacaridae. The first of these habitats is the old moat around Fort Hale in what is now Fort Hale Park, New Haven, Connecticut. This moat is triangular in shape with a perimeter of about 375 meters and is probably no more than two meters deep at its deepest point. The only communication with New Haven Harbor is through a floodgate which is kept closed, so that there is only a limited exchange between the water in the moat and the harbor at high tide. The salinity in the moat ($25.4^{\circ}/_{\circ\circ}$ on June 3, 1944) was insignificantly lower than that in the harbor ($26.0^{\circ}/_{\circ\circ}$), but the temperature was somewhat higher (27.0 compared with 23.8° C.). Several species of marine algae grow here and clumps of *Modiolus* are found around the margin of the water; and in other respects this is a typical marine environment, except that, despite its intertidal position, it is nontidal. Only *Copidognathus* (s. str.) *punctatissimus* and *Copidognathus* (*Arhodeoporus*) *arenarius* have been found here, and both of these are characteristically found below the intertidal zone, so their appearance in the moat is not surprising. More significant is the absence of *Metarhombognathus armatus americanus* and *Isobactrus setosus*, which are abundant in the harbor outside the moat. It is unlikely that this can be explained solely on the basis of high temperature, for *Copidognathus* (s. str.) *punctatissimus*, *Copidognathus* (*Arhodeoporus*) *arenarius* and *Metarhombognathus armatus americanus* are all known from Beaufort, where summer temperatures are little if any lower than in the Fort Hale moat.

The second example of this type of habitat is found at Beaufort, North Carolina, at the edge of Town Marsh, only 300 to 400 feet from the southern end of Piver's Island. Here a sand bar has blocked off a pool little more than three meters in diameter. At high tide this pool is in direct communication with freely circulating water in the channel between Town Marsh and Piver's Island. Because of the small size of the pool, the interchange of water between the pool and the channel at high tide must be significant, so that the temperature and salinity are maintained at the same level as in the channel. Several clumps of *Ostrea* were growing in this pool and were covered with a sparse coating of small but living *Enteromorpha* and filamentous green algae. Four species of Halacaridae were found here, *Rhombognathus*

TABLE VIII. DATA ON COLLECTIONS MADE IN FORT HALE MOAT, NEW HAVEN, CONN.

Sample No.		*Copidognathus* (s. str.) *punctatissimus*	*Copidognathus* (*Arhodeoporus*) *arenarius*
	October 9, 1943		
43–35	*Polysiphonia;* 42 g.	0	0
43–36	*Ulva;* 30 g.	0	0
	June 3, 1944		
44–65	*Ulva;* 40 g. 15,000 to 20,000 copepods, and 20,000 to 30,000 nematodes present	0	0
44–66	Algal scum from surface of water; ca. 10 g. Thousands of copepods and nematodes present	0	0
44–67	Sand below surface of water; 500 cc.	7	0
44–68	Sand just above surface of water; 500 cc.	0	3
44–69	*Polysiphonia;* 25 g.	25	0
44–70	*Modiolus;* imbedded in mud; 3; 7 to 8 cm. long	4	0

magnirostris lionyx, *Copidognathus* (s. str.) *acutus*, *Copidognathus* (*Arhodeoporus*) *arenarius* and *Agauopsis borealis* (Table XII), but *Metarhombognathus armatus americanus*, which was found in considerable numbers on *Ostrea* from Piver's Island, was not present.

The absence of *Metarhombognathus* and *Isobactrus* from these special nontidal habitats is significant when it is remembered that these two genera are also absent in subtidal habitats. The latter situation is shown in both the Long Island Sound and Beaufort collections, as well as in Viets' collections in the North Sea (1927a: 161, 166). Species of these two genera probably require periodic exposure to air in order to survive.[25] It is interesting to note that *Metarhombognathus* is present in the North Sea but not in the Baltic which is virtually nontidal. This absence may be due to the lack of an intertidal zone in the Baltic. If this is correct, then it would be necessary to assume that *Isobactrus setosus* was able to adapt itself more readily to the narrow wave zone, for this species is present in the Baltic. It is certainly much more agile than *Metarhombognathus* species, and this may be of value in maintaining the species along the restricted shores of the Baltic Sea.

[25] A parallel situation has been observed in *Hyadesia* sp. (Acaroidea, Hyadesiidae) at Beaufort and in Long Island Sound. This species is abundant in the intertidal zone where it occupies habitats identical with those of *Metarhombognathus armatus americanus*. It is not found below the tide zone, nor in the two special habitats discussed above. *Hyadesia fusca* (Lohmann) 1894 is known from the Baltic Sea.

Salinity and Local Distribution of Halacaridae

It is to be expected that habitats having markedly different salinities will differ in the composition of their faunae. Thus the number of species in an estuary decreases toward the upper end of the estuary until eventually the marine Halacaridae drop out entirely. Although the number of species is less than in marine habitats, the number of individuals is often very great.

In Table IX are given the records of samples taken in a tidal creek at Lighthouse Point, New Haven, Conn. Two points of particular interest are shown here. The first is that *I. setosus*, the dominant species of *Isobactrus* in Long Island Sound and Morris Cove, is replaced by *I. hutchinsoni*. It is not known how stable this condition is, so it cannot be stated definitely that *I. hutchinsoni* owes this local superiority to low salinity. However, considering the general abundance of *I. setosus* it is very likely that the predominance of *I. hutchinsoni* is due to the inability of the former species to compete with the latter at the salinities prevailing in this creek. The second point of interest is that the greatest population is developed in the lower one-fifth of the portion of the creek which was studied, where the salinity was around 12°/oo, and that the mites decreased in abundance from this point onward. At a point 1000 meters from the mouth of the creek, where the salinity was less than 1.0°/oo, no mites were found. The absence of the Halacarinae cannot be considered very significant, for like most tidal creeks, this one is very muddy, and generally it provided little opportunity for other than algicolous species to become established.

TABLE IX. DATA ON COLLECTIONS MADE IN TIDAL CREEK, LIGHTHOUSE POINT, NEW HAVEN, CONN., APRIL 7–19, 1944

Sample No.	*Habitat*	*Number of Mites*	
		Metarhombognathus armatus americanus	*Isobactrus hutchinsoni*
44–33	*Enteromorpha* and filamentous red algae, from mouth of creek; 14 g. Salinity 12.0 °/oo	2	0
44–18	*Enteromorpha* and filamentous green algae on grass stems, ca. 200 m. from mouth of creek; 22 g. Salinity 11.6 °/oo at low tide; 12.5 °/oo at high tide	210	50
44–37	Filamentous green algae, ca. 500 m. from mouth of creek. Salinity 4.2 °/oo at low tide	6	1
44–19	*Enteromorpha* and filamentous green algae in lateral drainage ditch; 5 g. Salinity below 1.0 °/oo at low tide; 1.5 °/oo at high tide	0	0
44–40	Filamentous green algae, 1000 meters from mouth of creek; 8 g. Salinity less than 1.0 °/oo	0	0

The poorness of the fauna at Solomon's Island, Maryland, is due in a large part to the low salinity there. One could reasonably assume that the fauna at the lower end of Chesapeake Bay should contain at least as many species as were found at Beaufort, N. C., with the possible exception of *Copidognathus* (s. str.) *acutus*. But only three species were found at Solomon's Island, where the salinity is generally 10–12°/₀₀.

The Fauna at Beaufort, North Carolina

The Beaufort collections are summarized in Tables X, XI and XII, and it will be necessary to point out only how they agree with the above discussion. The subtidal fauna is dominated by *Copidognathus* (*Arhodeoporus*) *arenarius*, just as is that of Long Island Sound. *Copidognathus* (s. str.) *septentrionalis*, however, is replaced by a new

Table X. Subtidal Collections Made at Beaufort, North Carolina, October 18–24, 1944. Various Substrates

Sample No.	*Locality and Substrate*	*Species*							
		Rhombognathus magnirostris lionyx	*Metarhombognathus armatus americanus*	*Halacarus (s. str.) anomalus*	*Copidognathus (s. str.) punctatissimus*	*Copidognathus (s. str.) acutus*	*Copidognathus (Arhodeoporus) arenarius*	*Agauopsis borealis*	*Total Halacaridae*
	Newport River, about 1 mile north of railway bridge, at 2.5 m.								
44–87	*Gracilaria;* 110 g.	—	—	—	3	9	2	—	14
44–88	Ascidians; 30	—	—	—	7	5	7	—	19
44–89	Mixed algae; 45 g.	—	—	—	7	—	10	—	17
44–90	*Gracilaria;* 83 g.	—	—	—	6	16	21	—	43
44–91	Hydroids; various species	—	—	—	39	66	99	1	205
44–92	Hydroids and ascidians	—	—	—	31	70	75	—	176
44–93	Broken, rough shells, perforated by *Cliona*	—	—	—	52	200	296	—	548
	About 1 mile southwest of Beaufort Entrance, at 10 m.								
44–109	Algal fragments; worm tubes	—	—	—	1	12	1	—	14
	East end of Harker's Island, just below low tide zone								
44–103	Brown algae; 150 g.	—	—	—	1	27	1	24	54
44–104	Mixed algae; 17 g.	—	—	—	—	4	2	6	12
44–105	Broken shells and fine sand	—	—	—	—	1	—	2	3
44–106	Sponges; 500 cc., loosely packed	—	—	—	8	50	1	53	112
	Piver's Island, on pier at Fisheries Laboratory, just below low tide zone								
44–107	Hydrozoa, various species; 1000 cc., loosely packed (20 cc. of amphipods and copepods)	—	—	—	1	4	3	—	8

TABLE XI. INTERTIDAL COLLECTIONS MADE AT BEAUFORT, NORTH CAROLINA, OCTOBER 18–24, 1944

Sample No.	*Locality and Substrate*	*Species*							
		Rhombognathus magnirostris lionyx	*Metarhombognathus armatus americanus*	*Halacarus* (s. str.) *anomalus*	*Copidognathus* (s. str.) *punctatissimus*	*Copidognathus* (s. str.) *acutus*	*Copidognathus* (*Arhodeoporus*) *arenarius*	*Agauopsis borealis*	*Total Halacaridae*
	Piver's Island (tidal amplitude about .7 m.)								
44–85	Silty sand in salt grass; mid-tide zone; filamentous green algae present; 200 cc.	1	135	—	—	—	—	—	136
44–97	Medium and fine sand; broken shells; 500 cc.	—	—	1	1	—	—	—	2
44–95	Medium and fine sand; 500 cc.	—	—	1	—	1	—	—	2
44–96	Very fine sand; 500 cc.	—	—	—	—	—	—	—	0
44–94	*Ostrea;* 25; av. length 6.5 cm. From south end of island where wave action is strongest; filamentous green algae virtually absent	—	—	—	1	6	4	—	11
44–98	*Ostrea;* 10; av. length 9 cm. From east side of island (sheltered); filamentous green algae abundant	—	75	—	—	—	—	—	75

TABLE XII. COLLECTIONS FROM TOWN MARSH, JUST SOUTH OF PIVER'S ISLAND, ON THE SHELTERED SIDE OF THE MARSH; IN THE HIGH TIDE ZONE, BUT IN A POOL FORMED BY THE BLOCKING OF A SMALL INLET BY A SAND BAR AND HENCE FILLED WITH WATER AT ALL TIMES

Sample No.	*Substrate*	*Species*							
		Rhombognathus magnirostris lionyx	*Metarhombognathus armatus americanus*	*Halacarus* (s. str.) *anomalus*	*Copidognathus* (s. str.) *punctatissimus*	*Copidognathus* (s. str.) *acutus*	*Copidognathus* (*Arhodeoporus*) *arenarius*	*Agauopsis borealis*	*Total Halacaridae*
44–101	*Ostrea;* 17; av. length 9 cm. Sparse coating of small, but living, *Enteromorpha* and filamentous green algae present	1	—	—	—	—	1	2	4
44–102	Coarse, broken shells; 1000 cc.	2	—	—	—	1	7	1	11

species, *Copidognathus acutus*. *C. punctatissimus* is the third most common species, as it is in Long Island Sound. The absence of *Metarhombognathus* from subtidal and other nontidal habitats is very noticeable and agrees with what has already been said about the local distribution of that genus. *Agauopsis borealis* was taken below the tide zone, whereas in Long Island Sound it was found in the intertidal zone. It is probably not restricted to either, but is most abundant just below the low tide zone. An extensive sand fauna is not developed, although occasional specimens of *Halacarus* (s. str.) *anomalus* are found. The fineness of the sand, most of it less than 0.25 mm. in diameter, would itself be a great barrier to the arenicolous species. *Copidognathus* (*Arhodeoporus*) *arenarius* is not arenicolous in the Beaufort region. With respect to the Beaufort fauna, it is a psammoxene form. This is probably true along a greater part of the coast between New Jersey and North Carolina, where the sand is too fine to provide a habitat for the Halacaridae.

ECOLOGICAL SUMMARY

1. A total of 41 species, subspecies and varieties of Halacaridae are recorded from North America and Greenland.
2. The Florida fauna is the richest on our eastern coast, that of New England is the second richest, and intermediate regions are the poorest.
3. There is no correlation between the New England-New Brunswick fauna and that of Florida.
4. The fauna at Beaufort, North Carolina, is more closely related to the northern than to the Florida fauna.
5. Nearly 70 per cent of the forms in the American Boreal Atlantic are identical with or closely related to forms in the European Boreal Atlantic. There is less relationship with the Mediterranean-Atlantic fauna, and virtually none with the Tropical fauna.
6. The transitional character of the fauna between Cape Hatteras and southern Florida is shown to consist more of a dropping out of certain Boreal genera and subgenera than of an overlapping of Boreal and Tropical elements.
7. The fauna of southern Florida is Tropical in character and is closely related to that of the Dutch West Indies and Bermuda.
8. The distribution of certain species or species groups in the Caribbean, Mediterranean and southwest Pacific regions suggests a Tethyian halacarid fauna parallel to that of other groups of animals.
9. *Rhombognathides*, *Metarhombognathus*, *Isobactrus*, *Thalassarachna*, *Arhodeoporus* and *Lohmannella* are shown to be nontropical, and the first three are characteristically Boreal or Arctic.

10. One of the most characteristic features of the Tropical fauna is the predominance of *Copidognathus* s. str.

11. The fauna of the subtidal zone is more uniform than that of the intertidal zone, especially from a qualitative standpoint.

12. *Copidognathus* (*Arhodeoporus*) *arenarius* is the dominant species in the subtidal zone in Long Island Sound and at Beaufort, North Carolina.

13. Limited collections near the eastern end of Long Island Sound suggest a transition from a eulittoral to a sublittoral fauna.

14. A well developed sand fauna consisting of three psammobiont and one psammophile species is found in Long Island Sound. The sand fauna of the American Boreal Atlantic is very similar to that of Europe.

15. Of the faunae developed upon molluscs, those on *Modiolus* and *Ostrea* are the richest and most complex. The encrustation of *Modiolus* by *Balanus* greatly increases the ability of this substrate to support an halacarid fauna.

16. The algicolous faunae are dominated by the Rhombognathinae; none of the Halacarinae are typically algicolous.

17. Observations on the absence of *Isobactrus* and *Metarhombognathus* from special nontidal habitats indicate that species of these genera require periodic exposure to air, thus accounting for their absence from subtidal habitats.

18. Habitats characterized by low salinity are also characterized by halacarid faunae containing a small number of species.

GLOSSARY OF TERMS

Some of the terms used in this paper are defined below, but in other cases only a reference to a labelled figure is given. Terms which have been applied to the Halacaridae for the first time are marked with an asterisk. References to species under which certain structures have been discussed more extensively are also given. A list of equivalent terms used by German workers has also been added, but this does not include those whose equivalence is obvious.

Accessory tooth. Fig. 207.

*Alveolus. Fig. 205. See rosette pore.

Ambulacrum. Fig. 211. All the structures lying beyond the tip of the tarsus, including carpus, carpite (if present), lateral claws, middle piece, and median claw (if present).

Anal papilla. Fig. 197.

Anal plate. Figs. 3, 7. The plate bearing the anus in those forms in which the genital and anal plates are separate.

Anterior epimeral plate (AE). Figs. 197, 198.

Antero-dorsal plate (AD). Fig. 197.

Anus. Fig. 198.

Apodemes. Fig. 198. These structures are frequently alluded to in the literature, but few workers seem to realize their true nature.[26] They are muscle insertions and are internal rather than external. They may be accompanied by invaginations of the cuticle (see *Copidognathus* [s. str.] *pachypus*, n. sp., and *C.* [s. str.] *caudatus*, n. sp.).

*Bacilliform seta. Any seta which is of nearly uniform diameter throughout and rounded terminally rather than tapering.

*Bacillum. Figs. 47, 207. A seta of variable form, usually bacilliform, just anterior to either the medial or lateral disti-dorsal seta of I-6 and II-6. The form and position of the bacillum is of taxonomic significance.

Base of capitulum. Fig. 202.

Camerostome. Fig. 198. The opening between AD and AE at which the capitulum is attached.

*Canaliculi. Fig. 205. See rosette pore.

Capitulum. Fig. 202. This includes the base of the capitulum, rostrum, palpi and chelicerae.

*Carpite. Fig. 25. A minute sclerite lying between the end of the tarsus and the middle piece of the ambulacrum, found only in the Rhombognathinae (and probably the Actacarinae). Its systematic importance has not been fully realized. See *Rhombognathus magnirostis magnirostris* and *Isobactrus setosus.*

*Carpus. Figs. 25, 211. The flexible portion of the leg between the end of the tarsus and the base of the claws. Fundamentally it is a thin-walled cylindrical membrane which is a direct continuation of the wall of the tarsus. The lateral claws and the middle piece of the claw (with or without a median claw) are attached distally. In the Rhombognathinae the carpite extends through the carpus.

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[26] Womersley (1937: 13–14) said of his new species, *Agaue hamiltoni*, "This species appears to be distinct from all other species and can be easily recognized by the "peculiar setae." The "peculiar setae" referred to are apodemes on the internal surface of AE! Viets (1940g: 66) again referred to these as "Borsten" (Viets' quotation marks).

Chelicera. Fig. 179.

Cheliceral membrane. Fig. 179. The pointed dorsal digit of the chelicera.

Claw fossa. Fig. 207. The inflection of the dorsal margin of the tarsus, distal to the disti-dorsal setae of the tarsus. The tarsi of nearly all species taper gradually, at least, but a fossa is present only if there is a noticeable inflection of the margin. Membranes may be present or absent.

Comb, or Pecten. Fig. 207.

Cornea. Fig. 197.

Costae (of PD). Fig. 197. The two central elevated ridges of the postero-dorsal plate.

Divaricate. Fig. 207. A term applied to the parambulacral setae when these are two-pronged. The members may be equal or unequal in size and form.

Epimeral pore. Figs. 198, 199. The large pores lying in AE, in the boundary between coxal areas I and II. This boundary is usually well marked in the lateral portions of AE by an internal ridge or external suture, or both.

Genital opening. Fig. 198. Generally this term has been used to refer to the circular or oval area, rather than to the slit-like opening itself.

Genital plate. Figs. 7, 76. The plate bearing the genital opening (or presumptive genital opening) in those forms in which genital and anal plates are separate.

*Genital sclerites. Fig. 198. Paired elongate sclerites lying within the membranous flaps covering the genital opening. In *Rhombognathides* and *Actacarus* they are enlarged and cusp-like.

Genito-anal plate. Fig. 198. The single plate enclosing both genital and anal openings.

Lateral claws. Fig. 207.

*Maxillary setae (rostral setae). Fig. 202. The term maxillary setae is preferable, because one of the two pairs may be on the base of the capitulum rather than on the rostrum. Furthermore, in species in which a third pair is added this pair is always on the base of the capitulum.

Median claw. Figs. 25, 207. A claw-like extension of the middle piece of the ambulacrum. It may be nearly as large as the lateral claws but is usually much smaller, or it may be absent. It may be unidentate or bidentate.

Membrane (of claw fossa). A lamellar distal or disti-dorsal expansion of the wall of the tarsus on one or both sides of the claw fossa.

Membranous area. Fig. 197.

Middle piece. Fig. 25. The chitinous sclerite to which the lateral claws are more or less firmly attached. In most species it is produced distally to form the median claw.

Ocular plate. Fig. 197.

Ostium (of rosette pore). Fig. 205. See rosette pore.

Palpi. Figs. 201, 202.

Panelling. Figs. 199, 200.

*Parambulacral setae. Fig. 207. The setae lying at the base of the ambulacrum on the sides of the tarsus. They are of characteristic form, and those on tarsi I and II are usually divaricate. See *Metarhombognathus armatus americanus*, n. subsp., and *Halacarus* (s. str.) *frontiporus*, n. sp.

Pectinate seta. Fig. 204. Any seta which is pectinate along one or two sides of the shaft.

*Pharyngeal plate. Fig. 202. The dorsal wall of the pharynx to which the dilator muscles are attached.

Porose panel. Fig. 199. A panel-like area, depressed or not, containing a number of pores.

Postero-dorsal plate. Fig. 197.

Posterior epimeral plate. Figs. 197, 198.

*Prebacillum. Fig. 47. A usually bacilliform seta lying anterior to the bacillum of tarsus I in certain genera. It has not been found on tarsus II in any species yet seen by the writer. In *Rhombognathus* it is longer than the degenerate bacillum, but probably in all other genera it is shorter. See bacillum. See also *Metarhombognathus armatus americanus*, n. subsp., and *Rhombognathus magnirostris magnirostris* Trouessart.

Rosette pore. Figs. 205, 206. A type of pore found only in *Copidognathus* s. str. (as redefined in this paper). Morphologically it probably represents a sunken porose panel (*q. v.*). Several types are known, but the pores in a given species are generally constant in form. Despite the fact that they are very promising systematic and morphological characters, they have been used very little, probably owing to a lack of understanding of their structure. A full morphological treatment will not be given here, but the typical rosette pore is described. Discussions of variations in structure can be found under the various species, especially *C. bairdi*, n. sp., *C. angustus floridensis*, n. subsp., *C. hummelincki* (Viets), *C. gracilis* (Viets), and *C. caudatus*, n. sp. The most elaborate type of rosette pore is diagrammed in Fig. 205. It consists of a central chamber, or alveolus, opening to the exterior by an ostium. Several canaliculi open into the alveolus, and these extend to the inner surface of the cuticle. In direct dorsal view the rosette pore appears as shown in Fig. 206. Although the canaliculi are represented in the same manner that one would represent a pore opening directly to the surface, it must be remembered that they open into the alveolus. However, occasionally a canaliculus does open directly to the surface. Variations in the rosette pores occur principally in the diameter of the ostium, the depth and diameter of the alveolus, the number and size of the canaliculi, and the uniformity or degree of perfection in the structure of the pores.

*Rostral setae. See maxillary setae.

Rostrum. Fig. 202.

*Subgenital setae. Fig. 168. Minute setae in or very near the small furrow (presumptive genital opening) just ventral to the genital suckers. They are usually visible only with oil immersion.

Triangle setae. Fig. 210. Three setae arranged in a triangular manner on the dorsal side of segments 3 and 5 of the legs. The base of the triangle lies near the distal end of the segment.

Equivalent Terms Used in German Writings

Aussenzinke	Accessory tooth.
Cilienkamm	Comb.
Excretionsporus	Anus.
Fiederborste	Pectinate seta.
Hornhaut	Cornea.
Kamm	Pecten; comb.
Krallengruben	Claw fossae.
Krallengrubenmembran	Membrane of claw fossa.
Krallenmittelstück	Middle piece (of ambulacrum).
Krallenzwischenstück	Carpite.
Längslinien; Längsbandern	Costae (of PD).
Mandibel	Chelicera.
Maxillarorgans	Capitulum.
Mittelkrallen	Median claws.
Ocularplatten; Okularia	Ocular plates (OC).
Palpengruben	Palpal insertions.

Postdorsalplatte	Postero-dorsal plate (PD).
Prädorsalplatte	Antero-dorsal plate (AD).
Rückenhaut	Dorsal membranous area.
Schnabel	Rostrum.
Seitenkrallen	Lateral claws.
Tasthaare (Lohmann 1889a: figs. 51, 55, 57).	Parambulacral setae.

DISPOSITION OF SPECIMENS

Specimens of all species seen in the course of this work have been retained in the writer's collection, but where duplicates are available they will be distributed as indicated below. A = author's collection, B = British Museum, London; P = Peabody Museum, Yale University; U = United States National Museum, Washington, D. C. The figures indicate the number of slides.

Rhombognathus magnirostris magnirostris, 2A, 1P; *magnirostris lionyx*, 1A.

Rhombognathides pascens, 8A, 1B, 1P, 1U; *seahami*, 7A, 1B, 1P, 1U; *mucronatus*, 3A, 1P, 1U; *merrimani merrimani*, 1A; *merrimani needleri*, 1A, 1P.

Metarhombognathus armatus americanus, 54A, 1B, 2P, 2U.

Isobactrus setosus, 16A, 1B, 2P, 1U; *levis*, 1A; *hutchinsoni*, 1A, 1P.

Halacarus (s. str.) *ctenopus*, 2A; *actenos*, 2A, 1B, 1P, 1U; *frontiporus*, 8A, 1B, 1P (*holotype*), 1U; *anomalus*, 1A.

Halacarus (*Thalassarachna*) *basteri basteri*, 5A, 1B, 1P, 1U; *longipes*, 2A; *balticus*, 24A, 2B, 2P, 2U; *subterraneus*, 7A, 1B, 1U; *capuzinus*, 7A, 1B, 1P, 1U.

Copidognathus (s. str.) *punctatissimus*, 12A, 1B, 2P, 1U; *acutus*, 16A, 1B (paratype), 2P (paratypes), 1U (paratype); *bairdi*, 4A, 1B (paratype), 1P (paratype), 1U (paratype); *curassaviensis*, 3A; *biscayneus*, 1A; *angustus floridensis*, 1A; *septentrionalis*, 3A, 1B, 1P, 1U; *gracilis*, 1A; *hummelincki*, 4A, 1B, 1P, 1U; *caudatus*, 1A; *pulcher*, 2A; *pachypus*, 1A; *bonairensis* 1A.

Copidognathus (*Arhodeoporus*) *arenarius*, 21A, 1B, 2P, 1U; *submarinus*, 5A, 1P, 1U.

Agaue nationalis, 1A.

Agauopsis brevipalpus brevipalpus, 5A, 1B, 1P, 1U; *borealis*, 3A, 1P, 1U.

Lohmannella falcata, 2A.

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STUDIES ON THE MORPHOLOGY AND SYSTEMATICS OF THE FAMILY HALARACHNIDAE OUDEMANS 1906 (ACARI, PARASITOIDEA)

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STUDIES ON THE MORPHOLOGY AND SYSTEMATICS OF THE FAMILY HALARACHNIDAE OUDEMANS 1906 (ACARI, PARASITOIDEA)[1]

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ABSTRACT

In this study the present status of the systematics of the Halarachnidae parasitic in Pinnipedia is summarized, the major deficiencies are indicated, and the points which must receive critical attention in the future are outlined. A number of misconceptions regarding certain structures, most notably the chelicerae, legs, tracheae and endosternite, are clarified and post-larval development is discussed. The existence of two natural species groups is demonstrated and the new genus *Orthohalarachne* is created for *Halarachne attenuata* Banks and its congeners. *Halarachne americana* Banks, *Orthohalarachne diminuata* (Doetschman) and *O. attenuata* (Banks) are redescribed and figured in detail. All other species are listed, and references, hosts and ranges are given. *Pneumonyssus* Banks is covered very briefly to complete the treatment of the family.

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INTRODUCTION

The principal objectives of this study are to consolidate our present knowledge of the systematics of the Halarachnidae parasitic in Pinnipedia, to indicate the major deficiencies, and to outline the points which must receive critical attention in the future development of the systematics of the family. Indeed, certain of the ideas set forth here will be found generally applicable to the solution of the peculiar morphological, systematic and biological problems presented by that heterogeneous group of Parasitoidea which inhabit the respiratory tracts of higher vertebrates.

Previously, all parasitic mites taken from the respiratory passages of Pinnipedia have been referred to the genus *Halarachne* Allman 1847, but detailed study of the morphology of these mites shows that there are two well defined and natural groups of species which differ consistently and in so many characters that they must be considered generically distinct. Accordingly, the new genus *Orthohalarachne* is created herein for those species congeneric with the type, *Halarachne attenuata* Banks 1910, which was the first described species of this group.

The references given for each species are not necessarily complete, but all papers having an important bearing on systematics and morphology are listed. All figures were drawn by the author with the aid of a camera lucida. Scales are given for most drawings and these can be used with reasonable confidence in obtaining measurements not given in the text. The scale for Figs. 1, 3, 10 and 28–31 represent 500µ, each division representing 100µ. In all other cases each subdivision of the scale represents only 10µ, so that a scale with three subdivisions equals 30µ, one with ten subdivisions is 100µ, *etc.* In all 100µ scales a longer mark has been made at the 50µ point.

Unfortunately the many gaps in our knowledge of the anatomy of certain of the species makes it impossible to provide a reliable key, but there are few species in the family, so that there is no particular necessity for a key at this time. Thus, there are at present four species of *Halarachne*, six of *Orthohalarachne* and seven of *Pneumonyssus*, a total of 17 species for the family.

FAMILY HALARACHNIDAE OUDEMANS 1906

Diagnosis. Dorsal plate of both male and female undivided, characteristically marked by insertions of muscles on inner surface (Fig. 18), finely and densely punctate. Tritosternum absent (see discussion under *Orthohalarachne diminuata*, p. 260). Sternal plate longer than broad; only 3 pairs of sternal setae present; metasternal setae absent. Jugularia absent. Genital opening of male at anterior margin of sternal shield. Genital opening of female a simple transverse slit between coxae IV. Rudimentary genital plate behind female genital opening; setae lacking in genital area. Coxae I–IV respectively with 2, 2, 2 and 1 setae ventrally. Three anal setae present as a rule, but sometimes 4 (the dorsal seta duplicated). Chelicerae 3-segmented. Digitus fixus of chelicera sometimes greatly reduced, shorter than digitus mobilis (Figs. 7, 38, 55, 60). Spermatophore bearer absent from male chelicera. A minute seta dorsally at base of digitus fixus. Epistome simple, triangular. Hypostome triangular and pilose. Maxillary palpi of adult with 4 segments, the tarsus and tibia fused. Tarsal prong bifid. Stigma lying above interval between coxae III and IV, or above IV, or even slightly behind IV. Peritreme very short, reaching only to level of posterior margin of coxa III, if that far. Peritremalia (Fig. 35) reaching to level of anterior margin of dorsal plate, but interrupted over coxa III. Tracheal system extensively developed, the stigmata of opposite sides joined by a transverse trachea.

Type Genus. Halarachne Allman 1847.

Remarks. Whether the above diagnosis is broad enough to include *Pneumonyssus* Banks 1901 cannot be stated, for the morphology of that genus has not been worked out completely, but the writer feels that it should be retained in the *Halarachnidae* for the present.

Morphological Observations. The following critical account of certain morphological aspects is presented in the hope that others will use it as a guide in clarifying the morphology of related genera, since it is only by such very detailed study that we can hope to arrive at a natural classification of the Parasitoidea. In the discussion the above diagnosis has been used as an outline. It should be remembered that the discussion applies primarily to *Halarachne* and *Orthohalarachne*, the only genera of the family of which the writer has firsthand knowledge. The extreme importance of technique has been pointed out, since many of the questions that still remain in the taxonomy and morphology of the group have their origin in improper or inadequate technique.

Sternal and genital plates. The outline of the sternal plate is difficult to determine except in properly prepared specimens, and yet it is of utmost importance that this plate be accurately delimited, especially with regard to its relationship to the sternal setae. There are numerous open questions in the taxonomy of the family which are due entirely to the failure of workers to clearly point out the extent of the sternal plate and the position of the sternal setae. For example, Ferris (1942: 79–80) was uncertain whether or not his *Halarachne miroungae* was identical with, or distinct from, *H. halichoeri*. His two published figures (1925: 163–167; 1942: 79–80) of the species omit the third sternal seta, the position of which is a critical character for distinguishing between *H. halichoeri* and *H. americana* (see p. 244). Doetschman (1944: 68–72) showed the female of *Orthohalarachne diminuata* (Doetschman) as having all three sternal setae outside the sternal plate, and yet it is clear from his description (p. 70) that he had difficulty in finding the outline of the sternal plate in the male. All this leaves considerable uncertainty about the accuracy of the description. This is unfortunate, for although there is no doubt that the forms described in the present paper (in which the sternal plate includes three pairs of setae) are *O. diminuata*, the highly interesting possibility of demonstrating subspeciation must be set aside because it is not certain that the sternal setae of Doetschman's specimens were really outside the plate.

The extent of the sternal and genital plates can be definitely established only by careful study of properly mounted specimens at high magnifications after the soft parts have been removed by a noncaustic hydrolytic agent (*e. g.*, trypsin) and the specimens then mounted in a medium of low or high refractive index (*e. g.*, glycerine or Hyrax, but not balsam or Clarite) for study at magnifications of 1000–1600. Staining is not only unnecessary but may result in erroneous observations. The extent of the lightly pigmented portion of the plates is deceptive, for the very margin of the plate is usually as colorless as the membranous area and can be seen only as a *change in texture of the cuticle*. In this connection it is important to note that it is impossible to properly treat material which has been in formalin, since the soft parts cannot be hydrolyzed; therefore, only alcohol should be used as a preservative.

The use of the genital shield of the female as a critical specific character (Finnegan, 1934: 326) is of questionable value, since the structure is weakly developed and highly variable in form and size, at least in *Orthohalarachne attenuata* (Figs. 43–53).

Chelicerae. There is considerable confusion with regard to the morphology of the male chelicera of *Orthohalarachne,* although the female chelicera is relatively simple and was correctly understood by Oudemans (1926d). In the female the tarsus (= digitus mobilis) forms the main distal portion of the chelicera (Figs. 38, 60) and bears an elaborate membrane on the dorsal surface. The digitus fixus, although reduced and modified, can be identified by its position and by the presence of the dorsal seta at its base. This seta is found in numerous genera of predaceous Parasitoidea in which the chelicerae are of more normal form, and in these genera the relation of the seta to the digitus fixus is the same as in *Orthohalarachne.* It should be noticed that the relative hypertrophy of the tarsus, as contrasted with the atrophy of the digitus fixus, has resulted in a ventral and medial displacement of the latter. The digitus fixus is bifid distally.

Turning to the male we find a similar situation (Fig. 36). There is a large tarsus which is identified by the apodemes of the levator and depressor muscles, and at the base of the tarsus is a structure which is similar to the digitus fixus of the female (compare Fig. 36 with 38). The base of this structure is somewhat more medially displaced than in the female, but the entire chelicera is hypertrophied as compared with that of the female, and this displacement is quite certainly associated with the hypertrophy. The distal portion of the structure is bifid, as is the digitus fixus of the female. Oudemans (1926d: 94, 105) considered that this two-pronged process in the male was the spermatophore bearer, with the digitus fixus represented by a small protuberance (Oudemans: fig. 88, *fi*). Oudemans misinterpreted this protuberance, for the closest study by the present writer reveals that it is only the point where the tarsus articulates dorsally with the basal portion of the chelicera. The + in Fig. 36 shows this swelling, in front of which is the articular membrane, each indicated by an arrow. Even overlooking the morphological evidence, it seems unlikely that such a highly adaptive structure as the spermatophore bearer would persist while the relatively conservative digitus fixus dropped out. Oudemans himself considered the "spermatophore bearer" (*i. e.*, digitus fixus) nonfunctional (p. 94, "Offenbar hat der wirklich Digitus mobilis die Funktion, die Spermatophore überzutragen, übernommen"). Of course, nothing is known of sperm transfer in the Halarachnidae, but Oudeman's surmise could very well be correct.

In summary, the present writer finds it impossible to accept Oudemans' interpretation of the structure of the male chelicera in *Orthohalarachne.* The "Spermatophorenträger" of Oudemans is the digitus fixus, while his "digitus fixus" is just a local thickening in the wall of the chelicera at the dorsal articulation of the digitus mobilis. A spermatophore bearer is completely lacking. Both males and females of *Halarachne* also have a digitus fixus (Oudemans 1926d: 82; figs. 17, 28); and the male lacks a spermatophore bearer. Although the chelicera of the female is normally oriented throughout, the distal portion of the chelicera of the male is rotated somewhat, and the hook-like tarsi oppose each other medially (see Oudemans 1926d: fig. 54). Dissected chelicerae compressed between coverslips are apparently twisted, because the basal portion is higher than wide, whereas the tarsus is wider than high. This torsion, while it results in an unnatural condition for *Orthohalarachne*, restores the primitive morphological relationship between the tarsus and the rest of the chelicera. This fact must be remembered while studying the figures of the male chelicerae in this paper.

The structure of the chelicera of *Pneumonyssus* Banks 1901 is still an open question, as it has not yet been accurately described or figured. Vitzthum (1931g: 59) stated of *P. simicola* Banks 1901, "Vom Digitus mobilis ist nichts erhalten als der ihm primär aussen seitlich angefügte Spermatophorenträger," which is interpreted by the writer as "Nothing remains of the digitus mobilis but the . . . spermatophore bearer." Although the present writer has not had the opportunity to study *Pneumonyssus*, he suspects that Vitzthum's interpretation of the structure of the chelicera was morphologically incorrect, for when accurate study is made it will probably be found that there is *no spermatophore bearer whatever.* Finally, the "hakenförmige Spermatophorenträger" of *Pneumonyssus duttoni* Newstead (see Oudemans 1935b: 502–503) is beyond all doubt the digitus mobilis and not the spermatophore bearer. Even if the digitus mobilis takes over the function and shape of a spermatophore bearer, it still remains the digitus mobilis, to which are attached the apodemes of the levator and depressor muscles!

Palpi. It is clear from the position of the tarsal prong in most Halarachnidae that tibia and tarsus have been fused, forming a tibiotarsus. Thus, in Parasitoidea with five-segmented palpi, the prong lies at the extreme proximal end of the short tarsus, whereas in *Ortho-*

halarachne and *Halarachne* it lies at the middle of the terminal segment, which is relatively very long (nearly twice as long as the preceding segment).

Legs. Doetschman (1944: 70) stated of the larva of *Orthohalarachne diminuata*, "The distal segments have false articulations plainly visible dorsally on legs II and III; this fusion results in a tibiotarsus." The latter part of the statement is incorrect, for a tibiotarsus is derived by the fusion of the tibia and tarsus (as in the palpi of *Halarachne* and *Orthohalarachne*). However, there is no suggestion of fusion of the tibia and tarsus in the legs. The tarsus is incompletely divided into two parts, the basal one of which is the basitarsus, the distal one the distitarsus.

Tracheae. In his original description of *Halarachne halichoeri*, Allman (1847: 49) stated, "One great transverse trunk (fig. 2g) passes across the posterior part of the cephalothorax, uniting the tracheary systems of opposite sides." But Oudemans (1926d: 54–55) disagreed with this, saying "Er muss etwas anderes für eine Trachee gehalten haben; vielleicht den vorderen Rand der nach vorn konvexen unteren Genitallipen, wenn man diesen Ausdruck gebrauchen darf." Allman was correct in his observation, for the present writer has found a transverse tracheal trunk in *Halarachne americana*, *Orthohalarachne attenuata* and *O. diminuata* (Fig. 54, shown by double row of dotted lines between the stigmata). Steding (1923: 453) also said that such a "Queranastamose" existed in *O. zalophi* (= *Halarachne otariae* Steding 1923), and was shown in her plate III, fig. 17, *Tr.* Reference to this figure shows no *Tr.*, but an error obviously had been made here. The "Dorsaldrüse" was labelled in fig. 16, but in fig. 17 "Ddr" indicated a structure which is thin-walled, oval in cross-section, and lies under the posterior end of the dorsal gland. This was undoubtedly meant to be *Tr*, since it is in the position occupied by the transverse trachea in *O. attenuata.*

In a dissection of *O. attenuata* a section of trachea was found which had been partly unwound, revealing its spiral structure (Fig. 21). This demonstrated that the tracheae of at least some Acari are essentially identical with those of insects in regard to the ctenidia. The spiral chitinous thread is continuous for considerable lengths.

The stigma lies in a small circular plate (the stigmal plate) from which extends the short peritreme. The stigma and peritreme are usually surrounded by a faintly outlined plate, the peritremalia, which extends from the level of coxa I to behind coxa IV, but is interrupted over coxa III. In *O. diminuata* the posterior portion of the peritremalia is very weakly developed.

Genus *Halarachne* Allman 1847

Diagnosis. Opisthosoma of gravid female saccate, not clavate (in forms known at present). Male and female with more than 4 pairs of setae dorsally between posterior margin of dorsal plate and anal plate; also ventrally, between level of coxae IV and anal plate. Digitus mobilis of chelicera of male tubular, sinuate in form, not forming a discrete hook; bearing a small dorsal lamella which is scarcely as broad as the tubular portion of digitus mobilis at same level (Oudemans 1926d: figs. 27–28). Maxillary palpi 4-segmented, the tarsus and tibia fused. Tarsal prong bifid. Adults with 4 pairs of maxillary setae ventrally (Fig. 5), including 2 pairs of small setae at tips of malae exteriores. Ventral surface of mala exterior without rudimentary seta. Larva and female (also male?) with 2 pairs of setae medially on P-2 (a total of 5 are found on the segment). Larva with dorsal anal seta longer than lateral anal setae; only 2 pairs of ventral maxillary setae present (those at tips of malae exteriores).

Distribution. North Atlantic Ocean; Pacific Coast of North America; South Orkneys (?); probably as widely distributed as the Pinnipedia, or at least the Phocidae.

Type. *Halarachne halichoeri* Allman 1847.

Synonyms. *Rhinixodes* Nehring 1884 and *Rhinacarus* Nehring 1884. Both were proposed as possible substitutes for *Halarachne* on the grounds that they were more appropriate.

Hosts. It is significant that there are no host records for *Halarachne* species outside of the family Phocidae. Oudemans (1926d: 108) stated "Ich habe mich davon überzeugen können, dass *Phoca vitulina* keine *Halarachne* birgt." We know today, of course, that *Phoca vitulina* does harbor *Halarachne*, at least in western North America.

1. *Halarachne halichoeri* Allman 1847 (but not of Ferris)

Thompson 1844, 291: *Halarachne halichaeri* Allman (nomen nudum). Allman 1847, 47–51: *Halarachne halichoeri.* Murray 1876, xi, 167–169: *Halarachne halichaeri* (Allm. 1847). Nehring 1884, 58–64: *Halarachne Halichoeri* Allman 1844. Steding 1923, 443, 448, 458, 474, 475, 488–490: *Halarachne Halichoeri* Allm. Ferris 1925, 163, 166: *Halarachne halichoeri* Allman. Oudemans 1926d, 49–86, 88, 90, 96, 99, 107: *Halarachne halichoeri* Allman 1847. Vitzthum 1929a, 4, 28: *Halarachne halichoeri* (Allman). Viets 1927b, 70–71: *Halarachne halichoeri* Allman. Finnegan 1934, 326: *Halarachne halichoeri.* Oudemans 1935b, 470: *Halarachne halichoeri* Allman 1847. Ferris 1942, 77–79: *Halarachne halichoeri* Allman 1847 (also misspelled *Halirachne*).

Distribution. Ireland to Baltic Sea.

Host. *Halichoerus grypus* (Fabricius), (Pinnipedia, Phocidae).

Remarks. Ferris has recorded this species from the Pacific coast of North America, but it is not clear from his work that this is correct. He compares Pacific specimens with *Orthohalarachne zalophi* (= *Halarachne zalophi*) and with *Halarachne miroungae* Ferris 1923. As is shown here, the former species is not even in the same genus, and Ferris' comparison of *H. miroungae* with *H. halichoeri* (?) is based on purely relative characters in which variations may be due either to individual differences or to age. Therefore, the existence of *H. halichoeri* on the Pacific coast has not been substantiated. The present writer prefers to refer all Pacific coast records to *H. miroungae* until more critical study shows that they should be treated otherwise. This problem is discussed further under *H. miroungae.* Ferris himself questions the specific identity of *H. miroungae;* hence he must question the validity of the characters upon which he based his comparison of *H. halichoeri* Allman, Ferris with *H. miroungae* Ferris.

2. *Halarachne miroungae* Ferris 1925

Ferris 1925, 164–167: *Halarachne miroungae* n. sp. Doetschman 1941, 23: *Halarachne miroungae* Ferris. Ferris 1942, 78–80: *Halarachne miroungae* Ferris 1925. ? Scheffer *et* Slipp 1944, 400: *Halarachne halichoeri.*

Distribution and Hosts. *Mirounga angustirostris* (Gill), (Phocidae): Guadalupe Island, off Baja California (ca. 29° N., 118° W.);

Phoca vitulina richardii (Gray), (= *Phoca richardii*): California (Pacific Grove, ca. 36° 28′ N., 122° W.); Washington (Nisqually, ca. 47° 15′ N., 122° 30′ W.). The Washington record is for *H. halichoeri* Allman, Ferris.

Remarks. The complexity of the situation in the Pacific *Halarachne* species is indicated in the following possibilities.

1. There is a single species, a) *H. miroungae*, or b) *H. halichoeri*.

2. There are two species, a) *H. miroungae* and an unnamed species, b) *H. miroungae* and *H. americana*, c) *H. miroungae* and *H. halichoeri*.

Of these, 1a or 2a is considered by the present writer to be most likely, with 1b and 2c highly improbable. There is at least one morphological clue which can be drawn from Ferris' work. Ferris (1925: fig. 1A; 1942: fig. 37b) showed the posterior end of the sternal plate reaching scarcely beyond the level of the posterior margin of coxa III, just as in *H. americana*. Oudemans (1926d: fig. 14) showed it reaching beyond the level of the anterior margin of coxa IV in *H. halichoeri*. This would indicate that the sternum of *H. miroungae* is smaller than the sternum of *H. halichoeri*, that the third pair of sternal setae lie outside the plate, and that therefore *H. miroungae* and *H. halichoeri* are distinct. However, in the form of the peritreme and the chelicerae, *H. miroungae* is closer to *H. halichoeri* than to *H. americana*.

3. *Halarachne americana* Banks 1899[3]

Banks 1899a, 212–214: *Halarachne americana* n. sp. Ferris 1925, 163, 166: *Halarachne americana* Banks. Oudemans 1926d, 49, 83–85: *Halarachne americana* Banks 1899. Finnegan 1934, 326: *Halarachne americana* Banks 1899. Ferris 1942, 78: *Halarachne americana* Banks. Doetschman 1944, 71: *Halarachne americana* Banks 1899.

Distribution and Host. Monachus tropicalis Gray (Phocidae). The type was collected from a zoo specimen. Finnegan (1934: 326) pointed out, " . . . it is doubtful whether one is justified in regarding the distribution of the host (West Indies, Coast of Yucatan to Florida and Bahamas) as established for the parasite." However, the fact that the species is distinct from both *H. halichoeri* and *H. miroungae* increases the probability that the host record is not misleading in this case, and that the distribution of *H. americana* is the same as for *Monachus tropicalis*.

The generic and family characters have been given in detail above and are not repeated in the following description of the species.

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[3] Through the kindness of Jos. Bequaert and Nathan Banks of the Museum of Comparative Zoology, the writer has obtained cotypes of *Halarachne americana* upon which this redescription is based. The specimens apparently had been mounted directly in balsam, for the surface of the body was covered with minute droplets of water. Although over 45 years old, the mites responded well to trypsin hydrolysis and were remounted in glycerine.

Female. The three females had the following dimensions (body length is dorsal length to base of capitulum):

	1	2	3
Body length	2866μ	2855	1855
Max. width, podosoma	1113	1113	tilted
Max. width, opisthosoma	1425	1450	tilted
Length, dorsal plate	1360	1427	1394
Max. width, dorsal plate	697	674	686
Ratio of L/W, dorsal plate	1.95	2.12	2.02

The third female (Fig. 1) is an adult but not yet completely mature. Fig. 3 shows the normal form of the distended female. The posterior portion of the dorsal plate, behind the level of maximum width, is relatively longer than in *H. halichoeri*. Only 3 pairs of setae are large enough to be seen, but dissections would probably reveal others.

Anal plate tending to be disti-dorsal in the gravid females but completely terminal in the nongravid female. Tritosternum absent. Sternal plate with only 2 pairs of setae, the third pair lying far outside the plate and more widely separated than the second pair in distended females (but not in the undistended female). The sternal plates of the three females measured 427 x 281, 416 x 280, and 450 x 292 μ (L/W = 1.52–1.54). Post-coxal apodemes approaching sternal plate, but not reaching it, and not forming pigmented horn-like processes of the plate. They are apparent only because of their refractility. Sternal plate not reaching beyond level of posterior margin of coxa III.

Ferris (1942: 78) said "An immediately noticeable feature of *halichoeri* is the appearance of the so-called 'endosternite' which is an internal sclerotization arising from the sternal plate between the coxae . . . forms four pigmented points." Ferris was referring not to the endosternite but to pigmented portions of the sternal plate. The endosternite in the Halarachnidae, as in all Arachnida, is an internal sclerite which has no connection with the sternal plate. Also, the writer knows of no Acari in which the endosternite is pigmented.

In *Halarachne americana* post-coxal apodeme III is so weakly developed that it could be mistaken for a fold in the cuticle. That behind IV is continuous with the peritremalia laterally and extends to the margins of the genital opening, where it joins with (or is produced into) a heavy spur-shaped apodeme, oriented longitudinally. Post-coxal apodeme IV lightly pigmented in the older female but simply refractile in the younger one. However, in all three the spur-like apodeme is reddish-brown.

In Fig. 10 the genital opening is gaping. The line just posterior to the sternal plate is the anterior margin; the other line is the posterior margin. The space between is the dorsal wall of the vagina. Genital plate variable in size and form. A median row of 6 to 7 pairs of setae between genital plate and anal plate, easily seen in young female but difficult to discern in older ones; some of them covered by secretions of the cuticular pores. Also, the opisthosoma is so greatly enlarged that the setae are relatively insignificant. Oudemans found a row of 6 pairs of setae in this position in the male of *H. halichoeri* but none in the female. Since young females of *H. americana* (in which the abdomen has the same form[4] as that of the males of both *H. halichoeri* and *H. americana*) have these 6 pairs of setae, just as in the male of *H. halichoeri*, the chaetotaxy of the opisthosoma is apparently identical in both sexes and in both species. Oudemans probably did not find the setae in the female of *H. halichoeri* because he had old distended specimens and not because the setae were absent.

The ventral cuticle of the opisthosoma is pierced by many cuticular pores (Fig. 14) which are found also on the dorsal surface as well as sparsely distributed over the podosoma. In young females nearly all these pores are clean; their walls are refractile and project slightly beyond the surface of the cuticle. In older females many of the pores are surrounded by irregular patches of a light brown secretion, especially abundant anterior and posterior to the stigmata at the sides of the body (Fig. 3). Here the secretions of adjacent pores sometimes coalesce to form small, irregular patches. In the two females seen,

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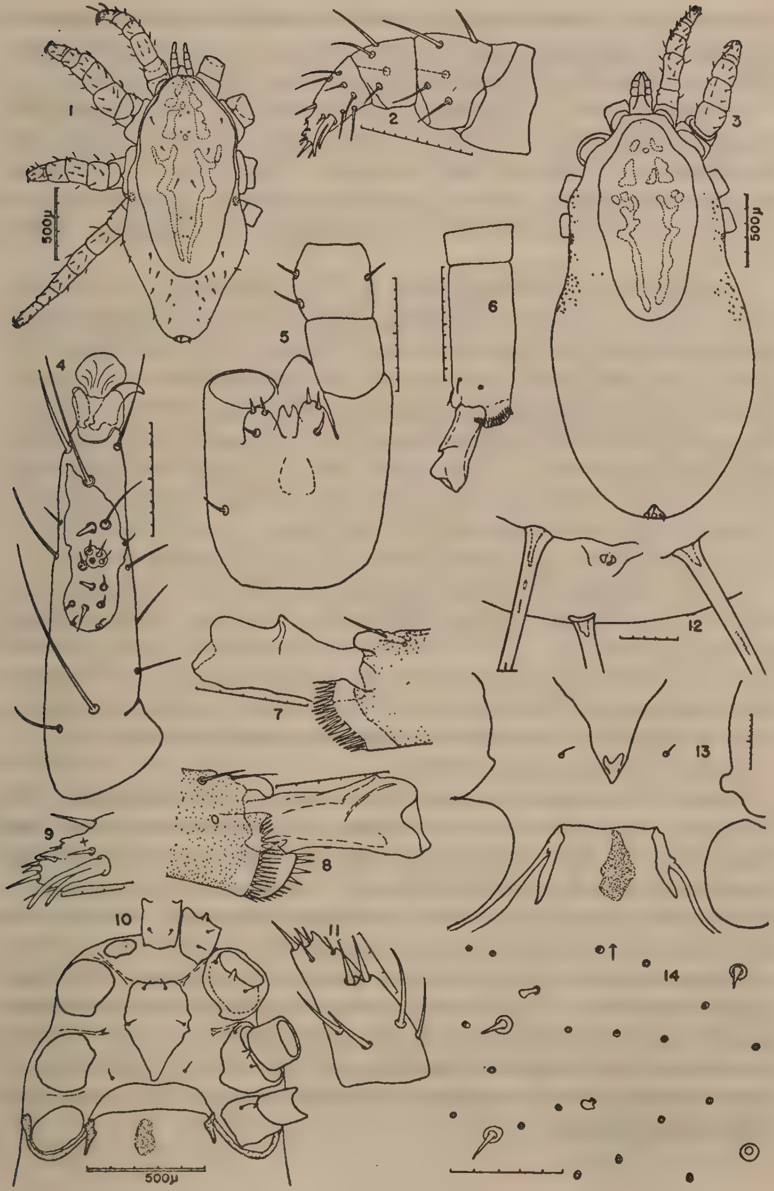
[4] Banks (1899a); also quoted by Oudemans (1926d: 84). "The male . . . is smaller than the female and the abdomen does not extend much beyond the dorsal shield, and is much narrower behind; . . ."

Figures 1–14. *Halarachne americana* Banks 1899. *1* Female: dorsum of young, undistended individual (scale = 500μ). *2* Female: palp, median view. *3* Female: dorsum of older, distended individual (scale = 500μ). *4* Female: left tarsus I, dorsal view. *5* Female: capitulum, ventral view (inclined distiventrally at angle of 18°). *6* Female: chelicera, lateral view. *7* Female: chelicera of young female, median view of distal portion. *8* Female: chelicera of older female, lateral view of distal portion. *9* Female: palpal tibiotarsus, median view of distal portion. *10* Female: podosoma of older individual (scale = 500μ). *11* Female: palpal tibiotarsus, lateral view. *12* Larva: posterior end of opisthosoma, ventral view. *13* Female: posterior end of sternal plate; genital opening; ventral view, young female. *14* Female: ventral surface of opisthosoma of undistended individual, about halfway between genital opening and anus.


500μ
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however, there is nothing approaching the condition in older females of *H. attenuata* where large portions of the body in the region of the dorsal plate are sometimes covered with grotesque, scab-like patches.

Peritremalia (Fig. 15) interrupted over coxa III. Stigmal plate not sharply delimited from peritreme. The latter crescentic in form, convex posteriorly. Stigma and peritreme within a deeply pigmented circular plate which is convex (seen from above). The peritreme in *H. halichoeri* is markedly different (compare with Oudemans 1926d: 73, 74).

Digitus fixus of chelicerae (Figs. 6, 7, 8) apparently even more reduced than in *H. halichoeri,* bearing a dorsal setiform projection which does not appear to be a true seta since it lacks a typical alveolus. The dorsal spiniform process on the tarsus can be identified with a similar process in *H. halichoeri* (see Oudemans 1926d: figs. 16–18). The portion of the tarsus beyond this process drops off sharply in *H. halichoeri* and bears a number of sharp teeth, but in *H. americana* the distal portion of the tarsus is as high as the basal portion and is not dentate in the two specimens dissected by the writer. One of these (Fig. 7) is the young female, the other is one of the older females (Fig. 8).

Ventral surface of capitulum as shown in Fig. 5. In the specimen drawn, one of the posterior maxillary setae is lacking. Palpi as shown in Figs. 2, 9 and 11. The + above the tarsal prong in Fig. 9 shows where an additional seta is found in one of the other palpi. Two spine-like projections of the dorsal surface of the tarsus present as shown, 3 setae terminally, the ventral one long, the dorsal ones short.

Male. Not seen by the writer.

Larva. Four larvae measured from 1439 to 1607μ in length. No characters of specific value were noted. The chaetotaxy of the body is as shown by Oudemans (1926d: figs. 1–2, *H. halichoeri*) with one slight and probably variable difference. Oudemans showed a postero-lateral pair of setae on both dorsal and ventral surfaces. In the larvae of *H. americana* both pairs are dorsal, but the most posterior of these (homologous with the ventral pair shown by Oudemans) is almost completely lateral. Anal setae with very heavy hyaline shafts, completely solid for much of their length, or containing at most a minute medulla which is frequently interrupted (Fig. 12), (the anal setae of *Orthohalarachne* are thin walled and hollow except in the distal 10 or 15% of their length).

4. *Halarachne* sp. Blanchard 1906

Blanchard 1906, 313: *Halarachne* sp. Steding 1923, 443: "Milben aus den Nasenhöhlen von *Leptonychotes leopardinus*, R. Blanchard." R. Blanchard is not to be taken as the author of *L. leopardinus.*

Distribution. South Orkney Islands (Orcades du Sud), (ca. 61° S., 46° W.).

Host. *Leptonychotes weddelli* Allen (= *L. leopardinus*). "Weddell Seal." (Phocidae, Cystophorinae).

Remarks. This species was not described by Blanchard (1906: 313) because he believed he had only larvae and "nymphs" ("Les larves hexapodes et les nymphes octopodes ont la plus grande resemblance avec celles de l'*Halarachne halichoeri* . . . Toutefois en l'absence des adultes; . . ."). Since there is no nymphal instar in the Halarachnidae, Blanchard's "nymphes octopodes" obviously were adults. It is not even certain that this species is a *Halarachne,* for nonattenuate specimens of *Orthohalarachne* could be mistaken for *Halarachne* if not examined closely. However, the fact that it was taken from a host of the family Phocidae is an indication that it belongs in *Halarachne,* for no species of *Orthohalarachne* has yet been reported authentically from the Phocidae. If this is a true *Halarachne* it is the only record of the genus (in the sense used in this paper) from the southern hemisphere.

Genus *Orthohalarachne,* new genus

Diagnosis. Opisthosoma of gravid female clavate in most forms; saccate in *Orthohalarachne diminuata.* Male and female with 2 pairs of setae dorsally between posterior margin of dorsal plate and anal plate, and also ventrally between level of coxae IV and anal plate. Digitus mobilis of chelicera of male forming a heavy hook and bearing a large foliaceous lamella which at its broadest level is twice as broad as the hook at the same level. Digitus fixus often bifid. Adults with only 2 pairs of long maxillary setae ventrally (Fig. 39) and a pair of rudimentary setiform structures ventrally on the malae exteriores (Fig. 20). Larva, male and female with only 1 pair of setae medially on P-2 (a total of 4 for the segment in the adult, and 3 in the larva). Larva with dorsal anal seta very short, much shorter than lateral anal setae, and often duplicated; no ventral maxillary setae present.

Distribution. North Atlantic Ocean, Pacific coast of North America, Falkland Islands.

Type. *Orthohalarachne attenuata* (Banks) 1910 (= *Halarachne attenuata* Banks 1910).

Hosts. Whereas *Halarachne* species have thus far been reported only from hosts of the family Phocidae, *Orthohalarachne* species are known only from hosts in the other two families of Pinnipedia, *viz.*, the Otariidae and Odobenidae.

1. *Orthohalarachne attenuata* (Banks) 1910[5]

Banks 1910a, 3, 12: *Halarachne attenuata,* new species. Oudemans 1926d, 50, 85: *Halarachne attenuata* Banks 1910. Finnegan 1934, 326: *Halarachne attenuata* Banks 1910. Ferris 1942, 78: *Halarachne attenuata* Banks 1910.

Distribution. Pribilof Islands in Bering Sea (57° 5′ N., 170° 25′ W.) to Depoe Bay, Oregon (44° 50′ N., 124° 5′ W.).

Hosts. *Callorhinus ursinus cynocephalus* (Walbaum), (Bering Sea and Oregon); *Eumetopias jubata* (Schreber), (Bering Sea), (Otariidae).

Type locality and host. The type data were given simply as (Banks, 1910a: 3) "Taken from a seal pup at St. Paul Island, by Mr. J. Judge, October 7, 1909." Oudemans (1926d: 85) incorrectly concluded that this is the St. Paul Island in the southern Indian Ocean (48° 35′ S., 77° 40′ E.), while Finnegan (1934: 326) assumed that this is the St. Paul Island of the Bering Sea, which is correct. Ferris (1942: 78) stated: "The host was in all probability the fur seal, *Callorhinus alascanus*, although it could have been a species of the genus *Phoca*, or of *Erignathus*." The latter two possibilities undoubtedly need not be

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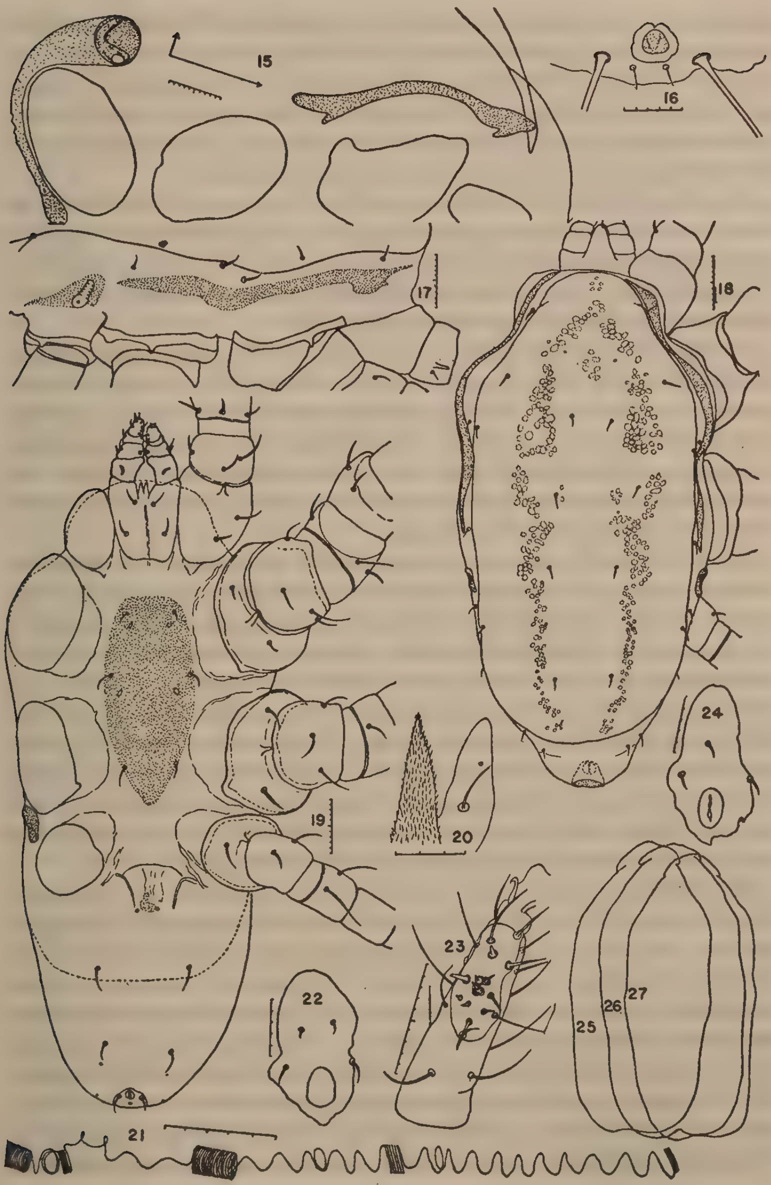
[5] V. B. Scheffer of the United States Fish and Wildlife Service collected the parasitic mites of seals on St. Paul Island on which are based the present morphological and systematic findings regarding the new genus *Orthohalarachne.* He has also provided the writer with the material from Depoe Bay, Oregon. The United States National Museum loaned the writer specimens of *Orthohalarachne attenuata* (Banks) 1910, taken from *Callorhinus ursinus* on "St. Paul Island, Alaska, from posterior nares of fur seal pup, 10 Sept. 1910" (data on slide).

Figure 15. *Halarachne americana* (continued). Female: podosoma, lateral view showing peritremalia, stigma, peritreme, *etc.*

Figures 16–27. *Orthohalarachne attenuata* (Banks) 1910. *16* Larva: anal region, ventral view. *17* Female (young, nonattenuate specimen): podosoma, dorso-lateral view. *18* Male: dorsum. *19* Female: venter. *20* Male: hypostome and mala exterior, ventral view. *21* Adult: trachea of dissected specimen. *22* Male: anal plate, posterior view. *23* Female (from *E. jubata*): tarsus I, dorsal view. *24* Male: anal plate, posterior view. *25* Female (from *C. ursinus;* St. Paul): dorsal plate. *26* Female (from *C. ursinus;* Oregon): dorsal plate. *27* Female (from *E. jubata;* St. Paul): dorsal plate.



considered. V. B. Scheffer stated (by letter) that "The seal pup from which the type of *attenuata* was collected was without question a first-summer fur seal. When seal is referred to on the islands, the name has only one meaning. The collector, James Judge, was for many years an agent in charge of sealing operations." This should remove all uncertainty as to the type locality and type host.

This species is redescribed from over thirty of several hundred specimens from the type locality and type host. V. B. Scheffer's collection also contains material of considerable interest in the life history of the Halarachnidae. The generic and family characters are not included, since they have been given in detail above.

Female. Body 930–4500μ long (Figs. 28–31), depending on age. Dorsal plate 899–978μ long, 427–472μ wide (L/W = 2.00 to 2.28), based on 10 females. Vertex setae absent. Other setae, panelling and pores as shown in Fig. 18. Anal plate (Figs. 22, 24) completely terminal as a rule; dorsal anal seta often duplicated as in larva. In one specimen there are 3 dorsal anal setae (in addition to the lateral setae) and a vestigial setal alveolus.

In the original figure the dorsal plate is represented by Banks as having a knob-like process at the anterior end and a deep notch at the posterior end. Both of these features are somewhat exaggerated in the drawing and variable in nature. In most specimens there is only a suggestion of a constriction at the anterior end under low power, but under high power it is seen that this is due principally to lighter pigmentation where these notches appear. The feature is more apparent in old individuals than in young ones. A posterior concavity is often present, but in no specimen has it been found as marked as in the original figures, and it may be completely absent. In the latter case the posterior margin of the plate is straight or slightly convex.

Tritosternum absent. In certain older specimens an indistinct, irregular patch of moderately refractile cuticle appears in the region between the anterior margin of the sternal plate and the capitulum, or there is sometimes a small fold here. It must be remembered that this area is subject to considerable flexion; local cuticular thickenings and folds are common in such regions. Also, numerous Parasitoidea with a tritosternum have other small sclerites developed in this region. There seems to be no logic in assuming, as some writers have, that a refractile area in this position must be a rudimentary tritosternum. The author prefers to consider that a tritosternum is completely lacking, since it has never been demonstrated that one exists in any of the *Halarachnidae*. Sternal plate including all 3 pairs of sternal setae and 2 pairs of pores. Post-coxal apodemes I, II and III very weak or absent; those behind IV continuous with the posterior portions of the peritremalia, in which are enclosed the stigmal plates and peritremata (Fig. 35). In young nonattenuate individuals this continuity is not apparent because the sclerotization is so feeble (Fig. 17). At the sides of the genital opening the post-coxal apodemes unite with, or are produced into, a pair of spur-like apodemes which project posteriorly (Fig. 28). Genital plate greatly variable in size and form (Figs. 43–53). A pair of rings lies either in or near the genital plate. Although variable, the genital plates of individuals from *Eumetopias jubata* are generally larger and more elliptical than in specimens from *Callorhinus ursinus*. This will be discussed below.

Setae of opisthosoma usually difficult to find in older females. Cuticle not pierced by pores of the type found in *Halarachne americana*. Portions of podosoma between coxae and dorsal plates covered by very irregular patches of a brown secretion. This is completely lacking in the youngest nonattenuate specimens; but in some of the older females virtually the entire dorsal and lateral surfaces of the podosoma are covered, although it is not deposited over the dorsal plate. Nothing is known of the nature of the secretion except that it is insoluble in alcohol, water, acetic acid, lactic acid and glycerine, but it is soluble in a dilute solution of potassium hydroxide (ca. 5%) at a temperature of 60–75° C. and hence it is not chitin. In a female with an abnormal twisted abdomen, about 20 brown concretions were seen inside the body cavity, distributed throughout its length, and seven of these were clustered on one side of a developing embryo. This apparently is the same material that is secreted on the outer surface of the body. Why it should be secreted internally is unknown, but at least this seemingly pathological case shows that the external secretion is, with little doubt, a product of the mite and not of the host.

Posterior portion of peritremalia distinct, almost completely enclosing the stigmal plate and peritreme. Ventral margin of stigmal plate characteristically exposed in all of the several specimens examined for this feature (Figs. 17, 35).

Digitus fixus of chelicera bifid, the dorsal membrane not projecting beyond the prominent, ventrally-inclined tip of tarsus (Figs. 33, 38). The general morphology of the chelicera has been discussed previously

(p. 239). Maxillary setae somewhat variable, especially the posterior pair, one of which is occasionally absent or displaced. Free portion of palpi as in male, except that trochanter does not bear a discrete process ventrally. The trochanter in Fig. 40 is probably higher than normal, owing to compression.

The lengths of the leg segments given below were obtained from a female in which the dorsal plate is 910μ long. The length of coxa + trochanter (c + tr) and of the ambulacrum (amb.) is the maximum length. In the other segments the dorsal length is given. Basifemur = bfe, distifemur = dfe, patella = pt, tibia = ti, basitarsus = bta, distitarsus = dta, total = T, ratio of the total length to the length of the dorsal plate = T/LDP.

	c+tr	bfe	dfe	pt	ti	bta	dta	amb.	T	T/LDP
I	250μ	48	114	117	117		——218——		864	0.95
II	266	48	96	122	101	67	106	93	899	0.99
III	266	48	74	125	101	67	104	101	886	0.97
IV	200	40	93	108	210	64	130	72	917	1.01

The above measurements were made from a dissected female from *Callorhinus ursinus*, Depoe Bay, Oregon (Slide no. 45–238–19). The basitarsus, distitarsus, and ambulacrum of leg I cannot be measured separately because of their structure, so only the total length is given.

Male. Total body length attaining 4500μ or more. Dimensions of dorsal plate as given for female. Essentially like female except in characters of ventral surface of podosoma and the mouthparts. The antero-lateral projections of the sternal plate shown in Fig. 42 appear to be exceptional since they are absent in other specimens, or greatly reduced. Genital opening completely anterior, or with a narrow strip of the plate anterior to opening. Opisthosoma uniformly cylindrical as in nongravid females.

Chelicerae as shown in Figs. 32 and 36, dorsal membrane of tarsus variable in length. Trochanter of palp with a discrete ventral process which is not bifid. The palp from which Fig. 37 is drawn is abnormal

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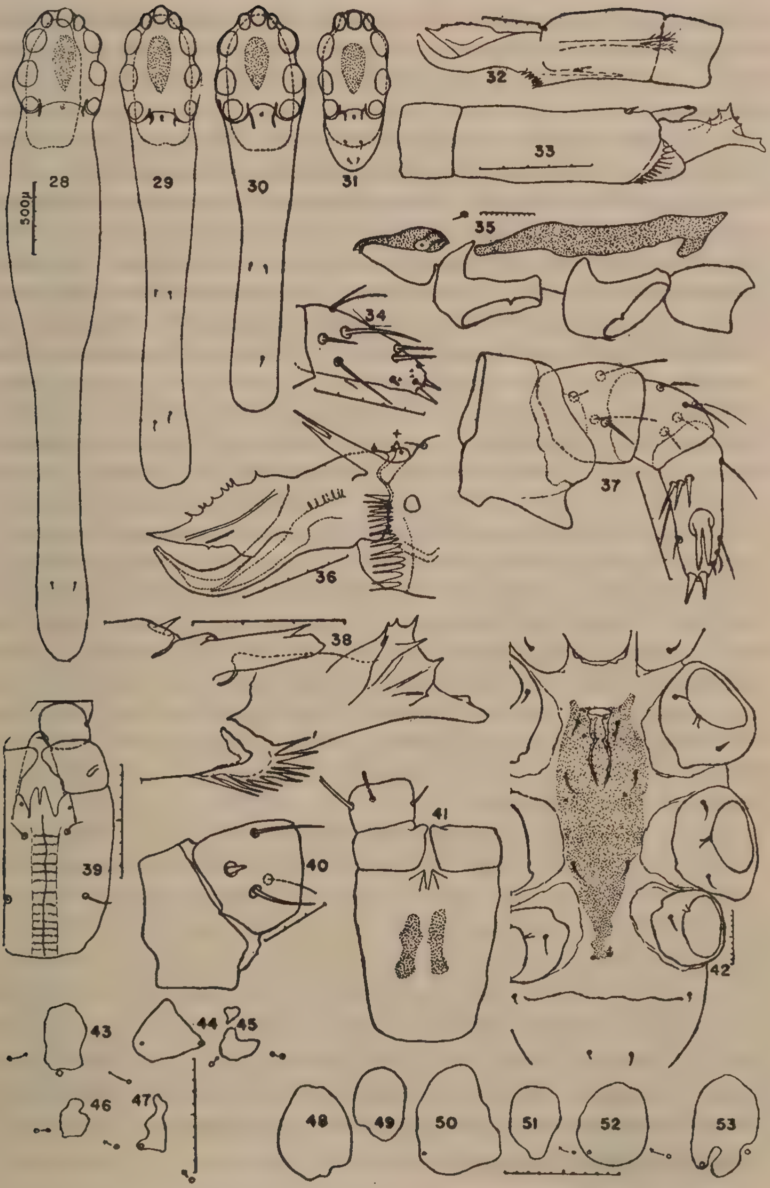
Figures 28–53. *Orthohalarachne attenuata* (continued). *28* Female (from *E. jubata;* St. Paul): venter (scale = 500μ). *29* Female: venter. *30* Female: venter. *31* Female: venter. *32* Male: chelicera, lateral view. *33* Female: chelicera, lateral view. *34* Male: tibiotarsus of palp, lateral view. *35* Male: podosoma, dorso-lateral view. *36* Male: distal portion of chelicera, median view. *37* Male: palp, median view. *38* Female: chelicera, median view. *39* Female: capitulum, ventral view. *40* Female: trochanter and femur of palp, lateral view. *41* Larva: capitulum, ventral view. *42* Male: venter. *43–47* Females (from *C. ursinus;* St. Paul): genital plate. *48–53* Females (from *E. jubata*; St. Paul): genital plate.


500μ

in that there are 5 setae on the patella (P–3). The posterior seta is absent from the opposite palp, as from both palpi of the five or six other specimens of both sexes that were examined closely for this character.

Larva. Body 1000 to 1100µ long (2 larvae). Dorsal anal seta often duplicated. No particular specific characters were observed.

Post-larval development. The development of the adult following the moult of the larval skin has long been a matter of conjecture. It has never been observed directly, and none of the authors who have published on the species of *Orthohalarachne* has been able to add much to our knowledge on the basis of preserved material. Oudemans, in 1926, could say only "Wenn ein Weibchen aus der Larvenhaut zum Vorschein kommt, ist es natürlich kurz; es wird dann, warscheinlich sehr schnell, anwachsen . . ." (Oudemans 1926d: 88, *O. zalophi*). The subject is of biological interest in itself, but it is also important because several questions of host relationship and taxonomy are related to it. For instance, Finnegan (1934: 326) pointed out the possibility that the type host record for *Orthohalarachne rosmari* is incorrect, since the type specimens were obtained from a walrus which had lived in the same basin occupied by the sea lions in Hagenbeck's Zoological Gardens in Hamburg, Germany. Finnegan stated, "One ought to add, however, that Dr. Oudemans, who described the species, is of the opinion that since the walrus and sea lions were only together for a few months 'it is scarcely admissible that in such a short time the Halarachnids of *Zalophus* should go over and propagate in the nasal cavities of *Odobaenus*'." (no reference is given by Finnegan for the quotation from Oudemans).

There is no evidence that the host record for *O. rosmari* is incorrect, but there is evidence that "a few months" is more than ample for cross-infection to occur. One of the lots of Halarachnidae collected by V. B. Scheffer was taken from a fur seal pup estimated to be two to four weeks old which was taken to the laboratory in a dying condition. The death of the seal was not caused by mite infestation, although this may have been a contributing factor, since "several dozen crawled from the nose as the pup was being examined."[6] *O. diminuata* was present here also. In all, 22 specimens of *O. attenuata* were taken from the nasal passages, 9 of which were nonattenuate (Figs. 18, 19,

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[6] Field note by V. B. Scheffer.

31) and 13 attenuate (Fig. 29). Of the latter, 8 were males and 5 were females. Each female contained an egg about 450μ long, the contents of which were densely packed and granular. There was no sign of segmentation. The longest female was 3540μ, whereas females containing larvae are 4000 to 4500μ long as a rule (body only). The base of the abdomen was not swollen as in the old females. Although these adults were no more than a month old, and possibly much less, they had bodies 80 per cent as long as in the larvigerous females, and contained eggs. The fact that host specificity appears to be weak in the Halarachnidae, in addition to the very short time required for infection and subsequent development, requires that all host records obtained from zoological park material be accepted with great reservation.

Other significant changes associated with age are: 1) an increased intensity of pigmentation, 2) deposition of the wax-like substance on the podosoma, 3) widening of the genital opening of the female, and 4) redistribution of the tracheae of the opisthosoma. With regard to the latter it must be noted that in nonattenuate females (Fig. 31) the tracheae of the opisthosoma form a knotted mass in the posterior end of the body cavity; but by the time the body has elongated to the stage shown in Fig. 30 the main longitudinal trunks have become straightened. The dorsal plate and legs of nonattenuate individuals are straw-yellow or nearly colorless, whereas in older individuals these are varying shades of brown or red-brown.

It has been realized for many years that there is no nymphal instar, although the evidence for this is only the consistent absence of nymphs. The "nymphes octopodes" of *Halarachne* sp. Blanchard 1906 must have been adults; the "nymph" of Ferris is the larva.

Variation. The specimens from *Callorhinus ursinus* are so like those from *Eumetopias jubata* that they must be considered as belonging to the same species. Evidence that subspeciation is under way is seen in the genital plate of the female, although the degree of overlapping that occurs does not seem to warrant the erection of subspecies at present. Figs. 43–47 show the genital plates of five specimens from *Callorhinus ursinus* chosen at random from specimens taken on St. Paul. Specimens from *C. ursinus* from Oregon likewise show reduced genital plates. Figs. 48–53 are of females from *Eumetopias jubata*, also chosen at random. It is not impossible, of course, that the differences in size are only ecophenotypic, resulting from host differences.

The geographical ranges of these two forms of *Orthohalarachne attenuata* overlap widely, but there is a certain amount of ecological isolation which is not perfect and apparently is not sufficiently strong, or the genetic stability of the species is too great, for clear-cut subspeciation to occur. It is not advisable to give names to these apparent semi-isolated breeding populations at present. The character of the genital plate is one which is purely relative, and parallel reduction could occur in populations which are only remotely related to one another. Accordingly, a situation could easily arise wherein two separate populations are placed together under one name, whereas they are less closely related to each other than to the original stock.

2. *Orthohalarachne reflexa* (Tubb) 1937

Tubb 1937, 417–418: *Halarachne reflexa*, sp. nov.

Distribution. Lady Julia Percy Island (ca. 38° 25′ S., 142° 3′ E.).

Remarks. The status of this form is uncertain at present, but it seems unlikely that it is a distinct species. Specimens collected by J. A. Tubb at the type locality in January of 1936 were kindly sent by Herbert Womersley of the South Australian Museum to V. B. Scheffer who in turn sent them to the writer for study. The lot contained nine females which could not be distinguished from females of *Orthohalarachne attenuata* taken from *Callorhinus ursinus* in the Pribilof Islands. Complete agreement is found in the extreme reduction of the genital plate and in the duplication of the median anal seta of some specimens. It is possible that further study, especially of males, will reveal differences of at least subspecific value, and therefore the name is retained here rather than being declared a synonym of *Orthohalarachne attenuata.*

3. *Orthohalarachne zalophi* (Oudemans) 1916

Oudemans 1916f, 312: *Halarachne zalophi* nov. sp. Steding 1923, 442–493: *Halarachne Otariae* n. sp. Oudemans 1926d, 50, 85–95, 98, 107–108: *Halarachne zalophi* Oudms. 1916. Finnegan 1934, 324, 326: *Halarachne zalophi* Oud. Ass 1935, 602: *Halarachne otaria* Steding. Doetschman 1941, 23: *Halarachne zalophi* Oudemans. Ferris 1942, 78, 79, 83: *Halarachne zalophi* Oudemans 1916. Doetschman 1944, 70: *Halarachne zalophi* Oudemans 1916.

Distribution. California (Pacific Grove, ca. 36° 38′ N., 122° W.; and San Diego, ca. 32° 45′ N., 117° 15′ W., in zoo).

Hosts. *Zalophus californianus* (Lesson) (= *Otaria californica*). *Eumetopias jubata* (zoo specimens). (Otariidae)

Remarks. The types of both *Halarachne otariae* Steding 1923 and *Orthohalarachne zalophi* (Oudemans) 1916 probably came from the same much-studied sea-lion head, and accordingly *H. otariae* is a synonym of *O. zalophi.* Steding's work was important from an internal anatomical standpoint, but her description of *H. otariae* contained no reliable features which enable us to distinguish two species. The possibility of synonymy was first mentioned by Finnegan (1934: 324) and was reviewed more in detail by Ferris (1942: 79). Ferris also noted the "strong possibility" that *O. zalophi* was identical with *O. attenuata,* and the present writer feels that this may eventually prove to be true. Judging from the large size of the genital plate of *O. zalophi* (see Ferris 1942: 83), it would resemble most closely the forms taken from *Eumetopias jubata* on St. Paul Island. However, it may represent a third semi-isolated population of *O. attenuata.*

Oudemans (1926d: 89) showed the third pair of sternal setae outside the plate, whereas in *O. attenuata* they are in the margin of the plate. His specimens were mounted in balsam, however, and it may have been that the margin of the plate was so transparent that it could not be seen. The writer has examined balsam mounts of *O. attenuata* in which it is impossible to discern the actual margin of the plate under any magnification or condition of lighting, and the same may have been true in the specimens seen by Oudemans. The fact that in a gravid female the third pair of setae remain less widely separated than the second (Oudemans 1926d: fig. 40) would suggest that they were still firmly held by the plate. In *Halarachne americana* this is not the case (Figs. 10, 13), and the posterior setae become more widely separated with distention of the body.

Ferris (1942: 79) stated, "Attention should be called to the strongly sclerotized and acute epistomal process and to the fact that the ventral side of the capitular base, which is composed of the fused palpal bases, bears two pairs of quite large setae and shows no trace of the lobes which appear in *halichoeri.*" The "lobes" are the malae exteriores which were unquestionably present in Ferris' material. They are much too conservative structures to be lost in this form, which is probably no more than subspecifically distinct from *O. attenuata,* if that (compare Figs. 5, 20, 39, 65). Ferris' drawing of the chelicera is not to be compared with the figures of *O. attenuata* in this paper, since it was drawn from a different view.

4. *Orthohalarachne rosmari* (Oudemans) 1916

Oudemans 1916f, 312: *Halarachne rosmari* nov. sp. Finnegan 1934, 321, 323–326: *Halarachne rosmari* Oudemans. Ferris 1942, 78: *Halarachne rosmari* Oudemans 1916.

Distribution. ? Franz-Joseph Land (ca. 81° N., 60° E.).

Host. ? *Odobenus rosmarus* (Linnaeus) (Odobenidae).

Remarks. This species was described from a walrus that had lived in a zoological park in Hamburg for seven years after it was collected in Franz-Joseph Land. On the basis of Oudemans' description and illustrations it appears to be distinct. The difference in form of dorsal plate in the male and female is exceptional, if accurately represented.

5. *Orthohalarachne magellanica* (Finnegan) 1934

Finnegan 1934, 321–326: *Halarachne magellanica* sp. n.

Distribution. Falkland Islands (ca. 52° S., 60° W.).

Host. *Otaria byronia* (de Blainville), "Southern Sea Lion" (*Otariidae*).

Remarks. Significant diagnostic characteristics of this species appear to be the relative shortness of the dorsal plate (L/W = 1.75–1.8) and the greatly enlarged trochanter of the male palp.

6. *Orthohalarachne diminuata* (Doetschman) 1944.

Doetschman 1941, 23: "new species" (no name given). Doetschman 1944, 68–72: *Halarachne diminuata* n. sp.

Distribution and Hosts. *Zalophus californianus* "California Sea Lion" (Otariidae); California. *Callorhinus ursinus* "Alaska Fur Seal" (Otariidae); St. Paul Island (57° 5′ N., 170°, 25′ W.).

Diagnosis. With all the generic and family characters listed above, in addition to the following.

Female: The two females have bodies 697 x 337μ (L/W = 2.06) and 809 x 416μ (L/W = 1.94). Whether the abdomen becomes attenuate in older adults is not known, but it probably does not. Some of Doetschman's specimens, which were even larger than those seen by

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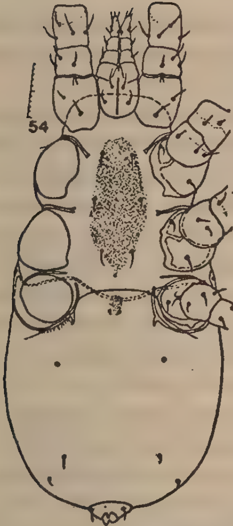
Figures 54–66. *Orthohalarachne diminuata* (Doetschman) 1944. All from *Callorhinus ursinus*, St. Paul Island. *54* Female: venter. *55* Male: distal portion of chelicera, median view. *56* Female: trochanter and femur of palp, median view. *57* Male: palp, lateral view. *58* Male: chelicera, median view. *59* Female: tarsus I, dorsal view. *60* Female: distal portion of chelicera, lateral view. *61* Male: tibiotarsus of palp, median view. *62* Male: venter. *63* Female: dorsum. *64* Female: chelicera, lateral view. *65* Adult: capitulum, ventral view. *66* Male: peritreme, stigmal plate and tracheae of left sides, lateral view.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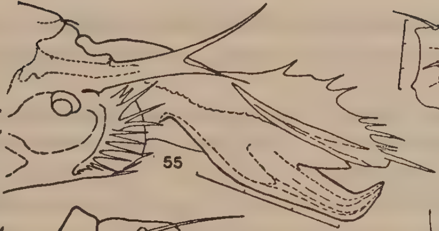
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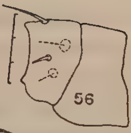
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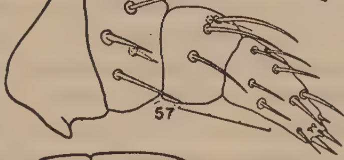
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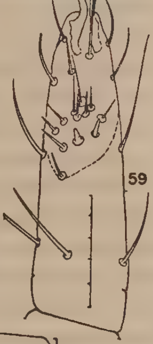
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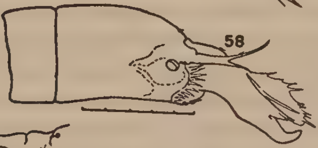
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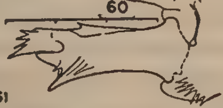
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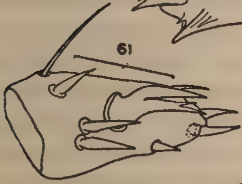
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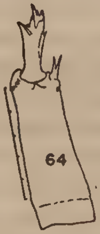
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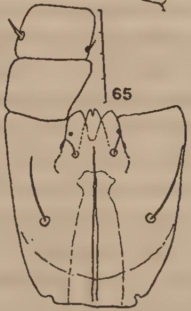
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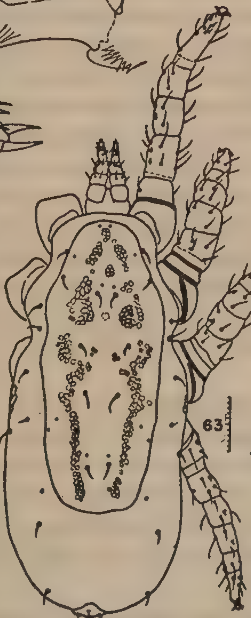
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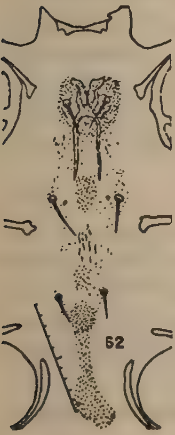
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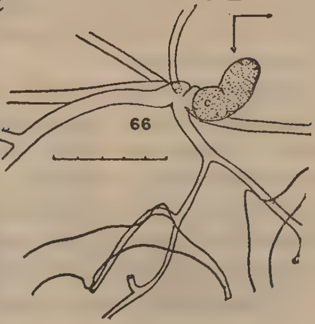
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the writer, showed no evidence of attenuation. Doetschman did not say whether any of the females contained embryos; those seen by the writer do not.

Dorsum (Fig. 63): dorsal plate 562 x 236μ (L/W = 2.38) and 575 x 242μ (L/W = 2.38). Using 900μ as the total length of the specimen shown by Doetschman (1944: fig. 1), the dorsal plate of his specimen is about 563μ long. Setae of dorsal plate conspicuous, 10 in number, other setae, pores and muscle insertions as shown in Fig. 63. Eight pairs of setae lie in the dorsal membranous area, making a total of 13 pairs of dorsal setae. There are usually 14 pairs in *O. attenuata*. The refractile rings near the postero-lateral angles of the dorsal plate are very near the position of the missing pair and may represent the vestigial insertion of these (compare Fig. 63 with Fig. 18).

Tritosternum lacking in both specimens. Sternal plate very faint, somewhat irregular in outline, appearing (in glycerine) as a faintly stippled area. In well digested material, at a magnification of 950 or greater, it can be seen that all 6 sternal setae lie within the plate, with the second pair more widely separated than the third pair. In one of the females the plate is rounded behind the third pair of setae, not pointed as shown in the figure. A pore lies behind only the first 2 pairs of setae. Stigma between and above coxae III and IV. Peritremalia (not shown in figures) as in *O. attenuata*, but extremely faint, especially the posterior portion surrounding the stigmal plate and peritreme. Four pairs of band-like post-coxal apodemes present. Delicate internal hair-like processes on apodeme IV show where muscles are attached. Apodeme IV continuous with posterior portion of peritremalia. Genital plate minute, with a pair of refractile rings which may represent the vestiges of setal insertions; setae absent in genital region. Another pair of refractile spots posterior to coxae IV. Anal plate completely terminal, dorsal anal seta showing no tendency toward duplication.

Chelicera (Figs. 60, 64) with dorsal membrane of digitus mobilis directed anteriorly and reaching beyond the heavy, ventrally-inclined tip. Digitus fixus bifid. Dorsal seta at base of digitus fixus so small it could scarcely be resolved, even at a magnification of 1600x. Palpi as in male, except for absence of the ventral apophysis on segment I (trochanter) and slightly smaller size (Fig. 56). Ventral surface of capitulum typical of the genus.

No particular specific characters were noted in the legs. Certain of the setae on the antero-dorsal surfaces of the segments are short and stout (Fig. 63), as in *O. attenuata.*

Male: Dorsal plate 562 x 254μ (L/W = 2.21); essentially as in female. Body alone 629 x 393μ (L/W = 1.60). Sternal plate virtually invisible at low magnifications. Under oil immersion, however, it is seen that a faint sternal plate with few scattered punctae is present, and this includes all 3 pairs of sternal setae. Two pairs of pores associated with the 4 anterior sternal setae; a pair of refractile rings at posterior end of plate between coxae IV. Differences in distribution of the punctae are shown in Fig. 62. Chelicerae and palpi as shown in Figs. 55, 57 and 61. The constancy of the bifurcation of the ventral digit of the tarsal prong (Fig. 61) is unknown. Leg I 540μ long, .96 as long as dorsal plate.

Remarks. There is no question that these two females and the male belong to this species. Considering that the specimens were taken from a different host, and even from a different zoogeographic province, it would be permissible to anticipate subspecific differences. Unfortunately the original description is not sufficiently detailed or accurate to permit a close comparison.

Doetschman made a comparison of the species only with *Halarachne americana*, stating, "There are many resemblances between *H. diminuata* n. sp. and *H. americana* Banks 1899." But this resemblance is artifical, consisting mainly of a somewhat similar body form and size, for there are 10 or 12 absolute characters listed in the generic diagnosis above in which the species differs from *H. americana*, while it shares every one of these characters with *Orthohalarachne attenuata.* Even the correspondence in size is fundamentally misleading, for *H. americana* is really larger than *O. attenuata*, despite the fact that it is shorter. The following measurements of representative specimens demonstrate this (all in micra):

	H. americana	*O. attenuata*	*O. diminuata*
Body length	2800μ	4500μ	740μ
Length of opisthosoma behind dorsal shield	1380	3500	190
Dorsal plate	1400	930	560
Length of podosoma	950	700	425
Diameter of coxa III	300	215	115
Max. width podosoma	1050	650	330
Max. width opisthosoma	1400	650	330

In all measurements but length of opisthosoma and total body length, *H. americana* exceeds *O. attenuata*, and thus *O. diminuata* more nearly resembles *O. attenuata* even in the relative character of size. This also demonstrates how misleading the single measurement, body length, can be. It is clear that *O. diminuata* is not to be compared with *H. americana*, but only with species of *Orthohalarachne*.

Genus *Pneumonyssus* Banks 1901

Oudemans (1935b) reviewed this genus and listed five species which he considered valid. Further reference to these can be found there. Subsequently, two new species have been placed here, so that the list is as follows:

1. *P. simicola* Banks 1901. Genotype.
2. *P. duttoni* Newstead *et* Todd 1906.
3. *P. congoensis* Ewing 1929.
4. *P. stammeri* Vitzthum 1930.
5. *P. dinolti* Oudemans 1935.
6. *P. procavians* Radford 1938.
7. *P. caninum* Chandler *et* Ruhe 1940.

Synonym. *Pneumotuber* Landois *et* Hoepke 1914. The genotype of *Pneumotuber* is *Pneumotuber macaci*, which is identical with *Pneumonyssus simicola*. The latter names have priority.

Remarks. The genus *Pneumonyssus* as it now stands will almost certainly require revision, since it apparently includes species of diverse phylogenetic origin. But although it seems unlikely that the genus is monophyletic, there is a considerable degree of morphological uniformity which is difficult to evaluate on the basis of present descriptions of the species, nearly all of which are inadequate if not inaccurate in several critical points. This morphological uniformity probably arises from two distinct causes, namely that (1) the habitats of the various species are similar, consisting of the respiratory tracts of various mammals, and (2) all of the species probably arose from species of external parasites which today would be placed in or near the families Liponyssidae or Laelaptidae. In other words, the predecessors of the present day *Pneumonyssus* species were all closely related both ecologically and systematically. The difficulties in the way of developing a system of classification that is both natural and convenient will be readily apparent to most workers in biology.

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